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AFRICAN MIMETIC BUTTERFLIES

BEING DESCRIPTIONS AND ILLUSTRATIONS OF THE PRINCIPAL
KNOWN INSTANCES OF MIMETIC RESEMBLANCE IN THE
RHOPALOCERA OF THE ETHIOPIAN REGION, TOGETHER
WITH AN EXPLANATION OF THE MÜLLERIAN AND
BATESIAN THEORIES OF MIMICRY, AND SOME
ACCOUNT OF THE EVIDENCES ON WHICH
THESE THEORIES ARE BASED

BY

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WITH TEN COLOURED PLATES AND A MAP

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PREFACE

OVER-SPECIALIZATION has been regarded as an evil, if a necessary one, not only in the domain of science, but also in the more commonplace pursuits of everyday life. Nevertheless, whilst it is given to the few to survey the problems of existence with that broad and responsive comprehension which has characterized the work of some of our greatest intellects, those of a lesser versatility may derive some comfort from the hope that their efforts to study one small point of interest may at least help to furnish a pebble towards the great fabric of truth which is arising out of the conceptions of the master architects of science. At the present time, when evolution is as much the basis of biological investigation as is the law of gravity of astronomical research, the study of mimicry has assumed a position of no little importance. Whilst the phenomenon may be regarded as merely a special expression of the value of colours and markings, it yet contains within itself many diverse forms, the common feature of which is their bearing on the struggle for existence, and the support they afford for the principles of organic evolution. The present work suffers from the already mentioned drawback of specialization, in that it deals only with a form of mimetic resemblance which obtains between butterflies of different genera, and that only with those of the Ethiopian region. Nevertheless, it is hoped that the information compiled from many sources will serve on the one hand to evoke a more general interest in a subject which has hitherto been in the hands of comparatively few workers, and on the other to stimulate further investigation which may lead to the elucidation of the many difficulties which still remain unsolved. Those who are familiar with the classification of butterflies may be inclined to find fault with the amount of space which has been devoted to purely elementary systematics; but I would remind those to whom such matters are familiar ground, that there are many potential naturalists who are at first attracted merely by the beauty of the objects they are moved to collect, and it is in the desire to provide for these and for the collector abroad all the information necessary to useful investigation that I have endeavoured to make the work complete in this respect. When years ago I became interested in mimetic phenomena, I found that any extensive knowledge of the subject was only to be obtained from a large and costly accumulation of the publications of various scientific societies, whilst familiarity with the appearance of some mimetic forms was, owing to their extreme rarity, a matter of considerable difficulty for the private collector. I have, therefore, endeavoured to compile into one volume the information contained in many publications together with drawings of specimens from several collections, and it is hoped that others may find in the result materials of some interest and a basis for further research.

In the matter of nomenclature I have followed as nearly as possible that of Professor Aurivillius in his '*Rhopalocera Aethiopica*', in the belief that the advantage of coincidence of arrangement with the only complete work on African Butterflies will outweigh whatever slight inconvenience may arise from lack of agreement in a few cases with more recent synonymy. I have not attempted to give all existing references to each species, but have endeavoured as far as possible to give the most important, including those of the first

published figures. It was not deemed necessary to have a special map produced for the comparatively small edition of this work. That bound up with the volume is the most recently published map of the African Continent, and though necessarily on a small scale will probably be found to indicate the position of most of the localities to which reference is made in the text.

Whatever deficiencies the work may present are certainly not due to lack of assistance. Its preparation has necessitated much correspondence with naturalists, both at home and abroad, and I feel that I cannot sufficiently express my indebtedness to all those who have with ready generosity placed all their resources at my disposal. It is almost impossible to mention in detail the many friends who have thus aided my scheme. Especially I would express my thanks to Dr. F. A. Dixey, Mr. H. H. Druce, Dr. Karl Jordan, Dr. G. B. Longstaff, Mr. G. A. K. Marshall, Mr. S. A. Neave, Mr. G. W. Smith, Commander J. J. Walker, and Colonel Yerbury, for valuable advice and assistance. My acknowledgements are due to Professor Aurivillius for permission to copy the figure of *Mimacraea fulvaria*, ♀ and to the publishers of Haase's 'Researches in Mimicry' for the like permission in reference to their figures of *P. dardanus antinorii*, forms *ruspinæ* and *niavioides*. I would express my appreciation of the painstaking manner in which Messrs. West, Newman & Co. have reproduced my drawings. Throughout the work they have courteously complied with every suggestion which could make for the improvement of the plates, with results which will, I trust, be considered eminently satisfactory. Lastly, there are two kind friends whose help I feel scarcely able to acknowledge in words. One is Mr. Roland Trimen, who in addition to affording me every encouragement since the inception of the work, has read through the whole of the original manuscript and offered valuable suggestions on many important points. Only those who have had experience of the unique knowledge possessed by the eminent author of 'South African Butterflies' can appreciate the advantage of such assistance to a much younger worker. The second is Professor E. B. Poulton. Few works on butterflies, and certainly none in connexion with mimicry, could be completed without reference to the many papers and essays which have emanated from his pen. Not only did Professor Poulton cheerfully grant me permission to make use of his own works on the subject, but he also afforded me every facility for access to the magnificent collections in the Hope Department at Oxford for the purposes of study and the drawing of the plates. In the midst of his strenuous round of work his invaluable advice and help have been always at my disposal, and it is with the deepest appreciation that I recall his many kindnesses.

For the rest, I commend the volume to those who have the taste and opportunity for pursuing an interesting study. To those who are unaccustomed to look to natural forces for instruction in the problems of life, the question of whether or in what manner so humble a creature as a butterfly may survive can seem but of small account. I hold, however, that no particle of knowledge is devoid of importance. Compared with the venerable ancestry of many even now surviving forms of life, Man is of very recent development. His greatest possession, the power of abstract thought, enables him to formulate theories and apply them to the problems with which he finds himself surrounded. Just as his physical attributes have been developed by a process of gradual evolution, so there must also be a mental or psychic evolution. It were rash to suggest a limit to the possibilities of scientific progress, and even the pattern of a butterfly's wing may be a not unworthy detail of the means whereby we may ultimately attain to that perfection of knowledge which shall one day reveal to us our own destiny.

CONTENTS

	PAGE
PREFACE	3
INTRODUCTION	7
I. DESCRIPTIONS OF MIMETIC ASSOCIATIONS IN AFRICAN RHOPALOCERA	24
II. ON OBJECTIONS WHICH HAVE BEEN RAISED TO THE THEORIES OF MIMICRY, AND THE EVIDENCE ON WHICH SUCH THEORIES ARE BASED	104
III. ON THE EVIDENCE THAT SOME BUTTERFLIES ARE MORE PALATABLE THAN OTHERS	109
IV. ON THE EVIDENCE THAT BUTTERFLIES ARE PREYED UPON BY BIRDS	120
V. GENERAL CONCLUSIONS	124
BIBLIOGRAPHY	127
INDEX	129
PLATES I—X	} <i>at end</i>
MAP	

INTRODUCTION

OF the great class Insecta, probably no section has been the subject of more careful and systematic study than that which includes the Lepidoptera, or scale-winged insects, popularly known as Butterflies and Moths. The Rhopalocera or Butterflies are somewhat unevenly distributed over the globe. Tropical America possesses by far the greatest number of described forms. Tropical Asia and the Indo-Malayan region come next in order, whilst Africa is comparatively poor in species. The latest complete work on the African Rhopalocera, that of Aurivillius, gives some 1,613 species, not including the *Hesperidae*, and with the present rapid exploration of this continent the number has already been considerably increased. Many years of patient and laborious work on the part of naturalists both at home and abroad have resulted, especially in recent years, in a better comprehension and definition of the relations existing between the various forms, and of the families and genera into which they may be separated.

The study of mimetic relationship which forms the subject of this work necessitates a knowledge of classification, and it is desirable therefore to give some account of the system, which, though subject to slight variations according to the views of different authorities, will nevertheless enable those who have not previously studied the subject to understand the terms used when differentiating between the various families, sub-families, and genera. The whole division Lepidoptera is divided into two sections, namely the Rhopalocera or those having clubbed antennae, and which are commonly known as Butterflies, and the Heterocera, which have the antennae of various other forms, and which are known as Moths.

The undesirability of having the larger of the two sections thus distinguished by a negative character has been outweighed by the convenience of the terms, though morphologically speaking the differences in the antennae are by no means so important as other though less superficially obvious distinctions.¹

The body of a butterfly is divided into three principal parts, the head, thorax, and abdomen. The head varies considerably in size, and carries, bilaterally placed, the large and conspicuous compound eyes. These are formed of many facets, each of which is practically a single eye or lens. The outer surface of the eye is more or less hemispherical, but each lens or facet appears to direct the light to one internal point so that the numerous images produced are coincident upon the retina. There are sometimes in addition two simple eyes placed on the back of the head and between the compound eyes. As these are generally covered with hairs, they probably have no visual function, but serve only to distinguish between light and shade.

The antennae are more or less elongated and many-jointed organs arising from the upper and anterior part of the head. They are of considerable importance in classification. What the precise function of these organs may be does not appear to have been satisfactorily elucidated, but it would seem almost certain that they have something to do with the

¹ I am aware that it is now proposed to revive the term Phalaenae proposed by Linnaeus for this section, but I have in this case retained the terms

here given as being more in accordance with common usage at the present time.

remarkable power possessed by the male insect of finding the female. This power is developed to a marvellous extent in certain moths (*Bombycidae*), and in these the male antennae are of unusually elaborate formation.

The mouth parts consist of a much reduced upper lip or labrum between the atrophied, or in some moths, partially atrophied, mandibles. Beneath this the trunk or haustellum is situated. This organ corresponds to the second pair of jaws or maxillae found in biting insects. It forms a tube through which the insect absorbs its food, and consists of two separable portions closely attached together. Beneath this the lower lip or labium carries the organs known as the labial palpi. These are three-jointed and are of importance in classification.

The thorax is the muscular centre of the body to which are attached the head, abdomen, wings, and legs. It corresponds to the second, third, and fourth segments of the larva, and these segments may be traced in the arrangement of the chitinous plates of which it is formed. The three pairs of legs are attached respectively to these three segments, and the wings to the second and third. Two small plates or *scapulae* are attached above the junction of the anterior wings.

The abdomen consists of nine segments, a rudimentary tenth segment being recognized by some authors, and carries seven pairs of spiracles, the orifices of the tracheae or breathing organs.

The legs, which are of great importance in classification, consist of three portions, the thigh or femur, the shank or tibia, and the foot or tarsus. The femur and tibia form two joints only, but the tarsus is five-jointed, the last joint being provided with claws, generally two in number. The front tibiae sometimes have a narrow appendage on the inner side and sometimes a claw-like appendage at the extremity. The two hinder pairs of tibiae are usually furnished with a pair of spines at the extremity, and in one family of butterflies (*Hesperidae*) the hinder tibiae have a second pair of spurs. In many butterflies the fore-legs are only imperfectly developed.

The wings are formed of a thin transparent membrane which is strengthened by a system of chitinous tubes called nervures and nervules. The front edge of the wing is named the costa, the side opposite to that the inner-margin, and the edge which lies furthest from the body is called the hind-margin. The angle formed by the costa and the hind-margin is the apex, that formed by the hind-margin and the inner-margin the posterior angle in the fore-wing, and the anal angle in the hind-wing. The point of attachment of the wing to the thorax is called the base.

One of the principal features used in classification is the neuriation, or arrangement of the nervures of the wings. These arise either from the base of the wing or from other nervures, in which case they are called nervules or branches.

Various methods of nomenclature have been proposed for these structures. That adopted here will be found to conform to most of the published descriptions. Fig. 1 shows the neuriation of the wing of a butterfly of the genus *Amauris*, and is somewhat similar to that found in the genus *Danaida*, from both of which genera come many butterflies which appear to form models for mimicry by those of other groups. Fig. 2 represents the wings of a butterfly of the genus *Hypolimnas*. In examining drawings of the wing neuriation of butterflies such as may be found in Messrs. Staudinger and Schatz's work on that subject, a great variety in the exact arrangement of the nervures will be observed, and these structures form the basis of the more minute classification. At the same time there is sufficient regularity of main nervures to enable a general system of nomenclature to be adopted. The following description applies equally to the two figures shown.

In the fore-wing the first nervure is a stout rib emanating from the base of the wing and extending some distance along the costa. This is the costal nervure and is without branches. Beneath this, and in close proximity, arises the subcostal, which usually gives off five branches, though in some cases a smaller number may be present. The last two branches form a kind of fork which stiffens the apex of the wing. Beneath is given off the median nervure which always has three branches. The distal ends of the subcostal and median nervures are united by two or three small cross nervules called discocellular, and designated respectively the upper, middle, and lower. The first is often much reduced, in some cases almost obsolete, and in others absent. The lower discocellular nervule is frequently absent or very rudimentary, especially in the hind-wing, the space between the subcostal

Fig. 1.

Genus *Amauris*.

Fig. 2.

Genus *Hypolimnas*.

C., Costal nervure; SC., subcostal; SC. 1, 2, 3, 4, 5, branches of subcostal; U.R., upper radial; L.R., lower radial; M. 1, M. 2, M. 3, branches of median; S.M., submedian; P.C., precostal; MDC., middle discocellular; UDC., upper discocellular; LDC., lower discocellular; D., discoidal cell; I., internal.

In the hind-wing UR. is the second branch of the subcostal in English nomenclature.

and the median, called the discoidal cell, being in these cases open at the distal end, a very noticeable feature in many genera. The area from the discoidal cell to the hind-margin is supported by two branches called the discoidal or radial nervules, which have been considered to be branches of a formerly existing discoidal nervure. Beneath the median is an unbranched nervure extending from the base to the hind-margin and known as the submedian. Beneath the submedian is a small nervure called the internal. This is a variable characteristic, being well developed in the genus *Papilio*, joined to the submedian in *Danaiida*, and absent in the great majority of other genera, including *Hypolimnas*. In the *Papilionidae* and *Morphinae* there is a small branch (in the fore-wing only) called the interno-median nervule. It joins the median and submedian nervures near the base. In the hind-wing the principal features are repeated but with some modifications. The costal corresponds to that of the

fore-wing. Except in the *Lycaenidae*, and some of the *Pieridae*, there is, close to the base, a short, curved, and usually simple precostal nervure. In some genera this nervure is forked, its lower branch being sometimes united to the costal, forming a minute prediscoidal cell. Some discrepancy exists between the English and German methods of naming the branches of the subcostal in the hind-wing, the second subcostal of English authors being called the upper radial in Dr. Schatz's work. Thus the nervule marked udc in the figure is regarded as the upper discocellular by the German nomenclature, and as the beginning of the second subcostal according to the English system. The essential difference between the two systems lies in the fact that while German naturalists count two radial nervules in the hind-wing the English system recognizes only one. In the hind-wing of the genus *Hypolimnas* and many others the discoidal cell is open as shown in the figure. The median nervure has three branches as in the fore-wing, and in addition to the submedian nervure there is the internal nervure which, though usually wanting or imperfectly developed in the fore-wing, is well developed and independent in the hind-wing, except in the *Papilionidae*, in which family it is absent.

Another system occasionally used is that in which all the nervules and nervures reaching the margin of the wing are numbered consecutively. In this system the posterior branch of the median is always numbered 2, the nervures below this being all called 1, and designated when necessary 1a, 1b, 1c, so that the corresponding nervures in front and hind-wings bear the same numbers. The nervures below the median are sometimes called branches of the internal, and in the German nomenclature the internal is called the inner-margin nervure. All these branches are sometimes called the anal nervures.

The wings of butterflies are covered with scales, to the structure and pigmentation of which their colours and patterns are due. These scales vary considerably in shape, but are essentially flat chitinous structures which may contain colouring matter between their upper and under surfaces, or the pigment may be intimately associated with the chitin. In some cases, as in the metallic colours of the *Morphinae*, the colours are due, not to pigmentation, but to minute striations on the surface of the scale, the intervals of which being shorter than certain of the wave lengths of light, cause what are known as interference colours. Each scale is attached to the wing membrane by a stalk, and its outer edge overlaps the points of attachment of the next scale. Many Lepidoptera have transparent wings, and this transparency is brought about in a great variety of ways. In some cases the scales are normal, but are devoid of pigment, in other cases they are set as it were on edge so that the light passes between as through an open blind, or they may be reduced to mere hairs. Certain moths emerge from the pupa with scaled wings, but the scales, owing to their feeble attachment, all fall off in the first flight. The colouring matter of the scales, at least in the *Pieridae*, has been shown by Professor Hopkins to be either uric acid or its derivatives, and it is noteworthy in this connexion that Schaeffer has shown that each of the hypodermal scale-forming cells contains an excretory vesicle.

The compilation of a satisfactory classification of the group Rhopalocera is beset with considerable difficulty, and various efforts in this direction have been productive of many systems and much difference of opinion. There is now, however, a considerable approach towards unanimity on the main lines of such classification, though differences still remain with regard to some of the details. For a long period the *Papilionidae* were placed at the head of the sub-order, and in so far as size may be a consideration, they would certainly merit that distinction. Bates, however, proposed a classification based on the structure of the legs, and especially on that of the tarsi of the front pair, and his arrangement still forms

the basis of modern systems. In view of the primary importance of the structure of the feet, I have prepared a plate showing the appearance of the tarsi of the front feet in the six principal groups of butterflies. The figures have been carefully drawn from photographs of specially made microscopic preparations, and a description of the special features in each case will be found on the page facing Plate I.

Regarding the butterflies as of higher development than the moths, Bates utilizes the more or less complete atrophy of the front tarsi as the principal sign of advancement. The first and highest family is the *Nymphalidae*, which may be described as four-footed butterflies, the front tarsi being only imperfectly developed in both sexes. This family is by far the largest. The second family is the *Erycinidae*, and in it the first pair of legs are still imperfect in the male, though complete but reduced in size in the female. The subdivisions of this family have been productive of some difference of opinion amongst systematists. For the sake of simplicity I have in the following table relied only on the palpi as distinguishing features, and so maintained only two sub-families as adopted by Dr. Sharp and by Professor Aurivillius. The third family comprises the whole of the *Lycaenidae*. In these butterflies the front legs are only a little smaller than the others, but in the male the tarsus is single-jointed, is covered with spines beneath, and has either no claws or only one. In the fourth, fifth, and sixth families the legs are perfect in both sexes. Many naturalists group the *Papilionidae* and *Pieridae* into one family with two sub-families, but the other structural features, notably the absence of the internal nervure in the *Pieridae*, are so distinct that it seems desirable to separate them more completely. The sixth family, the *Hesperiidae*, are in many features abnormal. In some respects they resemble moths more than butterflies. The bodies are large and the wings small, though the great rapidity of vibration of the latter gives the insects very remarkable powers of flight. The antennae are in most cases not truly knobbed at the end, but terminate in a hook. They are an exceedingly large family, upwards of two thousand species having been described, and they are already regarded by some authors as a separate sub-order under the name *Grypocera* (Karsch.)

The following table of classification has been compiled from various sources¹ and forms a summary of the principal recognized features of the various divisions.

Sub-order RHOPALOCERA.

- A 1. Antennae close together at origin ; tibiae of hind pair of legs with a terminal pair of spurs only.
- A. Front pair of legs much reduced in size in both sexes ; the tarsi in the male having only one joint, or sometimes rudimentary joints. In the female having usually five joints, but without claws. Pupa suspended by the tail and hanging freely.

Family I. NYMPHALIDAE.

- a. Discoidal cell of hind-wing closed.
- b. Fore-wing submedian nervure with a short fork at the base.
- c. Palpi short, slender, and divergent.
- d. Front foot of female ends in a knob.
- e. Larvae smooth with long fleshy tubercles.

Sub-family 1. *Danainae*.

¹ I am indebted to Trimen's 'South African Butterflies', 'The Cambridge Natural History', &c., for portions of the above and following information on classification.

AFRICAN MIMETIC BUTTERFLIES

- a. Discoidal cell of hind-wing closed.
- b. Fore-wing nervures frequently swollen at base.
- c. Palpi pressed together, not slender, and bearing long stiff hairs in front.
- e. Larvae thickest in the middle, posterior end bifid.

Sub-family 2. *Satyrinae*.

- a. Discoidal cell closed.
- b. Fore-wing submedian nervure not forked at base.
- c. Palpi cylindrical.
- e. Larvae armed with branched spines.

Sub-family 3. *Acraeinae*.

- a. Discoidal cell closed.
- b. Median nervure in fore-wing with short spur at the base.
- c. Palpi compressed, with scales at the sides and covered with hairs in front.
- d. Female fore-foot with a four-jointed tarsus.
- e. Larvae covered with branched spines.

Sub-family 4. *Heliconinae*.

- a. Hind-wing cell closed. Usually a small prediscoidal cell.
- e. Larvae not very spiny. Tail bifid.

Sub-family 5. *Brassolinae*.

- a. Hind-wing cell open.
- e. Larvae smooth or spiny. Tail bifid.

Sub-family 6. *Morphinae*.

- a. Fore- and hind-wing discoidal cells open or incompletely closed.
- d. Male front tarsus unjointed and without spines. Female front tarsus four- or five-jointed.
- e. Larvae spined or smooth.

Sub-family 7. *Nymphalinae*.

- B. Tarsi of first pair of legs imperfect in male, perfect in female.

Family II. *ERYCINIDAE*.

- c. Palpi short and small.

Sub-family 1. *Erycininae*.

- c. Palpi unusually long.

Sub-family 2. *Libytheinae*.

- C. Tarsi of front pair of legs perfect in female, but in male single-jointed, wanting one or both claws,¹ and spined beneath.

Family III. *LYCAENIDAE*.

- D. Tarsi of front pair of legs perfect in both sexes. Claws bifid, and provided with paronychia and pulvillus.

Family IV. *PIERIDAE*.

¹ Rarely, as in the African genus *Arrugia*, the males have jointed fore-tarsi armed with two claws.

- E. Tarsi of front pair of legs perfect in both sexes. Claws large and simple. Hind-wing without internal nervure. Tibiae of first pair of legs with small process.

Family V. *PAPILIONIDAE*.

- A 2. Antennae wide apart at origin. Tibia of hind pair of legs with two pairs of spurs. Tibiae of first pair of legs with process beneath.

Family VI. *HESPERIDAE*.

Turning from the structure and classification of the Rhopalocera to their individual features, our attention is drawn to the beauty and variety of their colours and patterns. Whilst some species, such as the glittering *Morpho cypris* of South America and the majestic *Ornithopteras* of the Indo-Malayan region, seem destined to represent the very climax of conspicuous splendour, others are coloured to harmonize so perfectly with their habitual surroundings, that they are sometimes visible only when actually flying. The collector's attention will early be drawn to the fact that in very many cases there is a great difference between the upper- and undersides of the wings. Even the dazzling *Morpho caca* is an inconspicuous object when the wings are closed in the position of repose and the steel-blue upperside is hidden. Our own comparatively sombre-coloured butterflies and moths provide ample study for this class of coloration. Our brightest butterflies, such as the Red Admiral and Tortoiseshell, are not easily seen when the wings are folded. Many British moths, such as the Crimson and Yellow Underwings, hide their brilliant colours when at rest by covering them under the grey or brown fore-wings. It is evident that whatever may be the purpose of the bright and conspicuous colours, it is nevertheless, in some cases at least, of importance to such insects that, when at rest and consequently less alert, they should be concealed. A little additional observation will bring to light a further and still more interesting discovery. Many Lepidoptera when at rest are not merely inconspicuous. They actually bear a marked resemblance to some of their inanimate surroundings. The common Brimstone butterfly, when settled with its wings closed, bears a curious resemblance to a holly leaf. Resemblance to leaves is one of the commonest features in the colouring of the underside of the wings of butterflies. It is carried out with the most wonderful perfection in the genus *Kallima*, sometimes known as the 'dead leaf' butterflies. In 'Science Gossip', 1867, p. 195, Wallace thus describes the appearance of *Kallima paralekta* in its native haunts :—

'It is a large and showy insect when on the wing ; the upper surface being glossed with blue and purple, and the fore-wings crossed obliquely by a broad band of rich orange. The under surface of the wings is totally different and is seen at a glance to resemble a dead leaf. The hind-wings terminate in a little tail, which forms the stalk of the leaf, and from this to the apex is a slightly curved dark-brown line representing the midrib. The transverse striae which cross the discoidal cell in many butterflies are here continued so as to form lateral veins, and the usual submarginal striae on the hind-wings, slightly modified, represent others towards the base of the wing. But it is only when the habits of the insect are observed that the disguise becomes manifested in all its perfection. This butterfly, like many others, has the habit of resting on a nearly vertical twig or branch, with the wings closed together so as to completely hide the upper surface. In this position, the little tail of the hind-wings exactly touches the branch, and we now see why it is always curved inwards a little ; for if

it were quite straight, it would hang clear of the branch and thus fail to represent an attached leaf. There is a little scallop or hollow on the margin of the fore-wings at the base, which serves to conceal the head of the butterfly, which is very small for its size, and the long antennae are carried back and hidden between the folded wings. When sitting on a twig in the manner described, the insect is to all appearance a perfectly dry leaf—yet it is evident that its chances of escape would be much increased if it were surrounded by real dry leaves instead of by green ones; for if, when pursued, it took refuge in a growing bush, it could hardly fail to be still a conspicuous object. Marvellous to relate, it does possess the habit of almost invariably entering a bush loaded with dead leaves, and is so instantly lost to sight, owing to its close resemblance to all the surrounding objects, that I doubt if the most vigilant flycatcher could detect it. I have myself often been utterly puzzled. I have watched it settle apparently in a very conspicuous situation, a few yards off, but on crawling carefully up to the spot, have been quite unable to detect any living thing. Sometimes while gazing intently, a butterfly would start out from just before my eyes, and again enter another dead bush a few yards off, again to be lost in the same manner. Once or twice only was I able to detect it sitting, and admire the wonderful disguise which a most strange combination of colour, form, and habits, enabled it instantaneously to assume. But there is yet another peculiarity which adds to the concealment of this species. Scarcely two of the specimens are alike in colour on the underside, but vary through all the shades of pale buff, yellow, brown, and deep rusty orange which dried leaves assume; others are speckled over with little black dots like mildewed leaves, or have clusters of spots or irregular blotches, like the minute fungi that attack dead leaves; so that a dozen of these insects might settle on a perfectly bare spray, and clothe it at once with withered foliage not distinguishable from that of the surrounding branches!

Resemblance to inanimate objects is not, however, by any means the only disguise which Lepidoptera are found to adopt. The undersides of the genus *Caligo*, from South America, present a beautiful portrait of the face of an owl, not only the great eyes, but every feather being exquisitely traced in the complicated pattern of the wings. The hind-wings also form a curious fold containing the body of the insect and projecting on the under side in such a way as to form a perfect representation of a beak; and though we have not, so far as I know, any such vivid description by an eyewitness as that just quoted, we may, I think, fairly assume that the appearance is coupled with habits which make use of and accentuate the extraordinary resemblance.¹ There is an Australasian moth which, when at rest, is almost indistinguishable from the head of a snake. Bates, in his 'Naturalist on the Amazons', writes: 'Along the narrow paths in the forests, an immense number of clear-winged moths are found in the daytime; mostly coloured like wasps, bees, ichneumon flies, and other Hymenopterous insects. Some species of the family have opaque wings, and wear the livery of different species of beetles; these hold their wings in repose, in a closed position over their bodies, so that they look like the wing-cases of the beetles they so deceptively imitate.'

¹ Since the above was written, Mr. W. F. H. Rosenberg has kindly given me some interesting particulars of the habits of these 'owl' butterflies. He informs me that the insects settle on tree trunks in the usual manner of butterflies, i.e. with the wings erect. The fore-wings are not hidden by the secondaries. In the dim light of the forest they are by no

means easy to see when thus at rest. They are not easily disturbed but are very alert, and after allowing one to come near start up with a 'mighty flap' of the wings, making the great eyes suddenly conspicuous. One could hardly imagine anything more startling to an attacking bird.

In view of the foregoing facts, the question naturally arises, what is the meaning of these resemblances in nature between a living creature, and in the one case some inanimate object, and in the other some other creature well known to be provided with formidable means of defence, or with equally formidable habits of offence? How have some butterflies, brightly coloured and conspicuous when flying, become enabled to completely efface themselves when at rest, and therefore less alert?

The doctrine of independent creation, involving the idea that the living things which exist around us were all separately created and brought into being just as we now see them, is one which has been so deeply impressed on the civilized mind, that the early existence of any alternative view may be easily overlooked. Nevertheless, long before the tentative efforts of early naturalists and philosophers culminated in the flood of light in which Darwin and Wallace expounded the mysteries of biological evolution, we find that there were those who sought to explain the formation of what we now call species by natural rather than supernatural agency. In spite, however, of many passages which may be discovered in pre-Darwinian writings, which seem to show an appreciation of some system of evolution, it was reserved for Charles Darwin to conceive the formation of species by natural selection, and to expound his argument by a wealth of instance and experiment which forms the subject-matter of his great work on the 'Origin of Species'.

The principles there explained are too well known to require recapitulation here, since they form the basis of biological study at the present day. What it is desired to emphasize is the fact that it is upon Darwinian principles that it is now sought to explain the colours and forms generally of living creatures, and in particular, that development of the widely exhibited phenomena of mimicry and protective resemblance of which this work treats.

The whole subject of animal coloration forms a most extensive and interesting study, and much valuable information on the subject will be found in Professor Poulton's work on 'The Colours of Animals'.¹ The terms proposed by that author have passed into regular use in dealing with the phenomena of mimicry, and it is necessary, therefore, to give some explanation of their meaning, for which account I am indebted to the work above mentioned.

Animals may be coloured so as to resemble some portion of their environment, which coloration may serve two purposes, namely, either to hide them from their enemies, or to enable them the more easily to approach their prey. In some cases both purposes may be served in the same animal. These two conditions have long been recognized as *Protective* and *Aggressive Resemblance*. Animals may, however, be so coloured as to resemble another species, the latter being distasteful or dangerous, or they may resemble some inanimate or unattractive object. These are known as forms of *Protective Mimicry*. On the other hand, a dangerous animal may be coloured so as to resemble an innocuous form, or an attractive inanimate object; these two phenomena constitute *Aggressive Mimicry* and *Alluring Coloration*.

In addition to these we have true *Warning* and *Signalling Colours*, by which animals give notice of their dangerous properties or provide an easy method of recognition for other individuals of their own species. Lastly we have *Sexual Coloration* or the colours which are displayed in courtship.

¹ 'The Colours of Animals; their Meaning and Use,' Poulton, 1890.

These types of coloration may be arranged as follows :—

I. APATETIC COLOURS.

Colours resembling some part of the environment or the appearance of another species.

A. Cryptic Colours.

1. Procryptic Colours.

Protective Resemblance. *Ex. The butterfly Kallima inachis resembling a dead leaf.*

2. Anticryptic Colours.

Aggressive Resemblance. *Ex. A mantis which looks like a leaf.*

B. Pseudosematic Colours.

1. Pseudoposematic Colours.

False Warning Colours. *Ex. A moth which resembles a hornet.*

2. Pseudepiseomatic Colours.

Aggressive Mimicry and Alluring Colours. *Ex. A mantis which resembles a flower and so attracts its prey.*

II. SEMATIC COLOURS.

1. Aposematic Colours.

True Warning Colours. *Ex. The well-known appearance of wasps, hornets, &c.*

2. Episeomatic Colours.

Recognition Marks. *Ex. The white tail of a rabbit.*

III. EPIGAMIC COLOURS.

Colours displayed during courtship. *Ex. The peacock's tail.*

This table is given in 'The Colours of Animals' in a much more extended form, but the above condensation will be found to suffice for the proper understanding of the terms usually met with in papers dealing with our present subject.

Inasmuch as the term *Pseudoposematic* conveys the idea of *false* warning colours it is hardly quite appropriate for cases of what will presently be described as Müllerian mimicry, for in these cases, although the coloration is intended to convey the false impression that an animal is of the same species as another which is really of a different kind, at the same time the colours of the former are as much a true signal of actual unpleasantness as are those of the latter. On the other hand the term *aposematic*, which is used to express true warning colours, does not simultaneously express the idea that in a Müllerian group the same colours are used as a warning by different species. Müllerian resemblance between two or more species is therefore known as *Synaposematic* coloration.

Our present study deals only with the resemblances which are found to occur between butterflies of different genera, and including in a few cases certain moths. It may be asked why butterflies should be selected as especially illustrating the course of evolution and natural selection. The reply is that insects, by their extraordinary adaptations and rapid succession of generations, afford probably more excellent and fruitful material for such investigations than do animals of other orders, whilst butterflies in particular, owing to the elaborate colour patterns of their wings, furnish the best guide to the study of those phases of development which, though in their case illustrated, as it were, by a series of wing pictures,

nevertheless are governed by the same influences as have guided the course of evolution in general. The value of the study of these insects was fully recognized by Bates, who, in the work already quoted, writes: 'On these expanded membranes nature writes, as on a tablet, the story of the modification of species, so truly do all changes of the organization register themselves thereon. . . . As the laws of nature must be the same for all beings, the conclusions furnished by this group of insects must be applicable to the whole organic world, therefore the study of butterflies—creatures selected as the types of airiness and frivolity—instead of being despised, will some day be valued as one of the most important branches of Biological Science.'

Bates's prophecy has been fulfilled, and it is singularly fitting that the great development of the importance of the study has been in connexion with those phenomena of mimetic association for which he himself, guided by Darwinian principles, was the first to offer an explanation.

In the case of the species of *Kallima* already described, and in that of the clear-winged moths, we see that the harmless and defenceless insect enjoys a certain amount of respite from the attacks of its insectivorous enemies by its possession of a more or less perfect resemblance either to an object in which its would-be captors have no interest, or to some creature which experience teaches is better left alone.

Having made the acquaintance of these facts we are in a position to consider a further, and in many ways more remarkable, development of mimetic association, and the one which forms the subject of the present work. The case may be broadly outlined as follows:—

It is found that many Lepidoptera resemble other insects of their own order though belonging to different genera. Butterflies of certain genera resemble other butterflies, or even moths, frequently widely separated from them in generic characteristics. Whilst in some cases such resemblances are slight, general, or, as it may be termed, tentative, in other cases they are carried out not only in the minutest particulars of colour and pattern, but also in similarity of habits and deportment.

H. W. Bates, who spent many years in collecting on the Amazon, was the first to call attention to this striking phenomenon, and at the same time to suggest an explanation, in a paper which was read before the Linnaean Society in 1861. In it he sets out certain interesting facts concerning the Lepidoptera of that region, and suggests as a cause, a process of natural selection which provides the strongest practical evidence in favour of the well-known Darwinian principles of evolution.

'The most interesting part of the natural history of the *Heliconidae* is the mimetic analogies of which a great many of the species are the objects.'

The sentence is a landmark in the study of the Lepidoptera, as it is from this point that the author begins his review of the facts of mimicry which came under his notice. The importance of the communication is such that it is desirable here to recapitulate the principal facts contained in this part of the memoir. When the numerous specimens collected had been classified, according to their structural characters, into their proper genera, it was observed that the superficial resemblance between butterflies of widely different genera was so marked as to call for some explanation beyond that of mere chance. This superficial resemblance had been noted by previous authors, but without any attempt at formulating a theory which would serve to explain the phenomenon. A great number of the species of the *Heliconinae* are accompanied in the districts they inhabit by generically different butterflies which bear a wonderfully accurate resemblance to them in shape, colour, and habits. The imitators belong to widely differing groups of Lepidoptera, such as *Papilio*,

Pieris, *Euterpe*, *Leptalis*, *Protogonius*, *Ithomeis*, *Castnia*, *Diopthis*, *Pericopis*, *Hyelosia*, and others; some of the latter genera belong to the Heterocera. Bates disposes of the possible question as to why these insects (*Heliconinae*) should be regarded as the imitators and not the imitated, by pointing out that whilst there is a general resemblance of type between the species of the genus *Heliconius*, the imitating insects depart more or less widely from their own family types, as though they had been perverted from their normal colour and markings in order to produce the resemblances noted. So accurate was the likeness between many of these forms that Bates remarks that in spite of his long experience he was never able to distinguish the *Leptalides* from the *Heliconinae* until after they were captured. The *Heliconinae* are exceedingly subject to local variation and modification, and it is important to notice that these local forms are accompanied by corresponding species or varieties whose markings continue to follow the design of the models. Apart from the fact already mentioned of the mimicking species being of a type unusual to their genera, Mr. Bates points out that in most cases the models are excessively abundant, whilst the mimics are very rare. Thus the *Leptalides* were to the *Ithomiæ* which they imitated, in the ratio of about 1 to 1,000. The *Heliconinae* are also imitated by several species of moths. Bates, after carefully studying the subject, found that 'those features of the portrait are most attended to by nature which produce the most effective deception when the insects are seen in nature'. The resemblance is not always very striking when the insects are seen in the cabinet, but the author acknowledges that he was constantly deceived when capturing these insects in the woods. Having noted some of the well-known instances of insects resembling in form and colour inanimate objects which are of no interest to their pursuers, the author puts forward the suggestion that the *Heliconinae* which are the objects of so much imitation by other butterflies are in some way naturally protected from their vertebrate enemies, and that therefore the mimicking species escape, owing to their superficial resemblance to such protected forms, and he suggested that their protection lies in the fact of their unpalatability. He remarks that in the whole course of his experience he never saw the *Heliconinae* attacked by birds, lizards, or other predaceous creatures, such as the *Asilidae*,¹ whilst butterflies of other families were frequently pounced upon by such enemies. He also noticed that they all had a peculiar smell, and that the captured specimens were always less subject to the attacks of vermin.

As previously stated, his explanation of the origin of these mimetic analogies is based on the theory of natural selection. The suggestion that the *Heliconinae* were in some way protected did not explain the observed fact that some members of the same group are themselves the imitators; in other words, they 'counterfeit each other'. This phenomenon is one of which at that time no explanation was forthcoming, but the subject was dealt with in a paper by Dr. Fritz Müller in May, 1879, a translation by Professor Meldola being published in the Proceedings of the Entomological Society of the same year. This paper deals with a specific case of mimicry between *Ituna ilione* and *Thyridia megisto*. The two genera are considered to belong to the *Danainæ*, and both possess distasteful qualities. Müller points out that although the two genera are closely related, the resemblance is not due to consanguinity, but has been acquired by imitation, in support of which conclusion he refers to the fact that their progenitors, judging from the large number of existing species, presumably had the wings covered with scales, and not transparent as in these two cases. It may be noted here in parenthesis, that the resemblance, mainly caused by the transparent

¹ In view of more recent research, it seems probable that the *Heliconinae* are in fact preyed upon by the *Asilidae*. See Poulton, Trans. Ent. Soc., 1902, p. 336.

areas of the wings, has been shown by Professor Poulton not to be due to consanguinity inasmuch as the transparency is brought about in the two species by entirely different means. A microscopic examination shows that in *Thyridia* the scales are very short, and each alternate scale has been reduced to a very narrow form almost like a hair. In *Ituna* the scales are still of normal size but are widely separated. Had the transparency been due to close relationship, it is reasonable to suppose that it would have been produced by the same structural formation in both species.

Müller continues his remarks in pointing out that both species may be assumed to be protected from the fact that both emit a repugnant odour ; the organ by which this is produced in *Thyridia megisto* being a tuft of hair placed on the upperside of the hind-wing on the subcostal nervure, and is present in both sexes, though not so well developed in the female, the case being probably one of transmission of a male characteristic to the female sex.¹

Taking the case as undoubtedly one of mimetic resemblance, the author proceeds to consider the question as to which of the species is the original form and which the imitator. In this instance the problem is not one which is easily solved, since both insects appear in about equal numbers, or at least one does not predominate sufficiently to be regarded as the model. Again, though *Thyridia* possesses a somewhat larger number of similar allies than does *Ituna*, neither insect appears to depart sufficiently from the 'family facies' to enable it to be regarded as the imitator. Both species being apparently distasteful, there is again nothing to serve as a guide to the desired distinction. The Müllerian explanation of the phenomenon of resemblance between two species of protected genera depends on the assumption that insectivorous birds, lizards, &c., do not instinctively know what is good to eat and what is distasteful or injurious. That the assumption is well founded I shall endeavour to show later on. Meanwhile it is desirable to quote here the words of Professor Meldola's translation of Müller's paper describing the advantage gained by mimicry between two already protected butterflies.

'Now if two distasteful species are sufficiently alike to be mistaken for one another, the experience acquired at the expense of one of them, will likewise benefit the other ; both species together will only have to contribute the same number of victims which each of them would have to furnish if they were different. If both species are equally common, then both will derive the same benefit from their resemblance—each will save half the number of victims which it has to furnish to the inexperience of its foes. But if one species is commoner than the other, then the benefit is unequally divided, and the proportional advantage for each of the two species which arises from their resemblance is *as the square* of their relative numbers.

'For instance, let us suppose that in a given region during one summer 1,200 butterflies of a distasteful species have to be destroyed before it becomes recognized as such, and that in this region there exist 2,000 individuals of one (*A*) and 10,000 of another (*B*) distasteful species. If they are quite different, each species will lose 1,200 individuals ; but if they are deceptively alike, then this loss will be divided among them in proportion to their numbers, the first (*A*) will lose 200, and the second (*B*) 1,000. The former (*A*) accordingly gains 1,000 (or 50 per cent.) of the total loss, and the latter (*B*) only 200 (or 2 per cent.) of this number. Thus while the relative number of the two species is in the ratio of 1 : 5, the advantage derived by those possessing the resemblance is 25 : 1.²

¹ The fact that these glands are not now considered to be necessarily the seat of distasteful qualities does not affect the argument.

² The precise mathematical statement of the case is somewhat complicated. See Blakiston and Alexander. 'Nature,' 1883, pp. 481-2, and 1884, pp. 405-6.

‘If two species are concerned, of which the one is very common and the other very rare, then the advantage falls almost entirely on the rarer species. If, for example, *Acraea thalia* were a thousand times commoner than *Eueides pavana*, the latter would derive a million times greater benefit from the resemblance of the two species, whilst for the *Acraea* the benefit is practically *nil*. Thus *Eueides pavana* might by natural selection be converted into one of the most exact mimics of *Acraea thalia* although it is just as distasteful as the species imitated. On the other hand, if two or even several distasteful species are about equally common, resemblance brings them a nearly equal advantage, and each step which the other takes in this direction is preserved by natural selection—they would always meet each other numerically, so that finally one would not be able to say which of them has served as the model for the others. . . . To this category *Ituna* and *Thyridia* may belong, although the first has probably made the greater step in passing from the former dissimilarity to the present resemblance of the two species.’

Such is the theory of what is now known as Müllerian mimicry, a phenomenon which will be found to be of the greatest importance in its bearing on many of the complicated cases of mimetic association which are now recognized.

A careful study of Müller’s paper is the more interesting from the fact that he to some extent suggests that the adaptations which take place between two species of distasteful genera may be mutual; that is to say, both species may be modified so that an ultimate type of pattern may be produced which is not necessarily that of the original in either species. This theory has been greatly developed by Dr. Dixey whose paper on mimetic attraction (Trans. Ent. Soc., 1897) forms a most valuable contribution to the literature of the subject. For the purpose of his argument the author takes certain forms of South American *Pieridae* which have developed patterns closely mimetic of various species of *Heliconinae*. Starting with a *Pieris* of ordinary appearance it is shown that only a very small modification, such as might easily arise as a variation, is sufficient to give the butterfly an approximate resemblance to a certain Heliconine species. This slight variation persists as a separate species of *Pieris*, but by further slight modifications, also persisting as species, forms appear which come to resemble other species of *Heliconinae*. In this manner we can see actually existing a series of modifications by which the original form of *Pieris* is drawn along different lines of attraction, and so produces several mimetic species, the extreme forms of which differ widely from each other, though reached by very gradual modifications; and it is further pointed out that the forms which in these cases appear to act as models are not themselves isolated, but are members of large groups, all the individuals of which have a similar type of coloration, and which may be considered to form Müllerian associations. As is well known, distasteful butterflies are usually so coloured as to appear conspicuous in their habitual surroundings, and in the case of a species having the necessity of profiting by its distasteful qualities, it may either develop a conspicuous pattern of its own, or adopt that of some already well-known and dominant form. The latter development, as might be expected, appears to be the commoner, since it benefits all the species of the dominant group, and the benefit being mutual, there are good grounds for expecting the model to itself assist in the resemblance, by undergoing a certain amount of modification in the direction of the mimic. To quote the author’s own words, ‘Every conspicuous and distasteful form is a centre of attraction for other forms, whether edible or inedible; but in the former case (Batesian mimicry) the mimetic attraction is limited in operation, and acts only in one direction, influencing nothing but the mimic; while in the latter case (Müllerian mimicry) the mimetic attraction is unlimited and mutual, acting

reciprocally in both directions and influencing each member of the group.' And again, in a further passage, 'The respective value of the attraction exercised or suffered by any member of a Müllerian group will depend on its numbers, its nauseous qualities, and its notoriety. The stronger any species is in these respects the stronger will be its power of attraction, and the weaker in comparison will be any force tending to draw it in the direction of other members of the group. The actual mimetic path taken by any species will be the resultant of the forces acting upon it. If the form happens to be a dominant one, these external forces will be insignificant in comparison with its own stability ; and it will therefore resist change to a large extent or perhaps altogether. The most complete intermingling of characters given and taken on both sides may be expected when two species meet on equal terms, neither being strong enough to predominate over the other.'¹ Obviously convergent mimicry, where it occurs, confers a benefit on more individuals than does the mimicry of a distasteful by an innocuous species, for in the latter case only one species is assisted in the struggle for existence. Indeed, if the edible species become numerous they naturally form a positive menace to the protected kind, so that from the nature of the case Batesian mimicry usually exists in cases where the model is abundant relatively to the mimic. That this need not, however, necessarily be so, has been pointed out by Marshall in a letter to Professor Poulton² in which he instances the case of the resemblance between *Euralia mima*³ and *Amauris echeria*. The writer describes the latter insect as 'Probably the best protected butterfly here' (Natal), and continues in the following words, 'Supposing they occur in equal numbers in a given area, and that certain birds, by chancing to catch three or four of the former in succession, were induced to prey upon butterflies with that coloration, then, from a mathematical standpoint, every alternate specimen caught by any bird would be *A. echeria*. Now I think we are quite safe in assuming that the fact that every other butterfly caught had a nauseating taste and smell would be far and away more likely to create a strong and lasting impression upon a bird's mind than the fact that every second one proved to be edible, and would be quite sufficient to deter the bird from attempting to eat butterflies of that colour. This is from a mathematical standpoint solely, but from what I know of these two forms in life, I believe that, presuming them to occur in equal numbers, a larger proportion of *echeria* would actually be captured, for *mima* is a much more shy insect, and although it has the same slow sailing flight (when undisturbed) it does not keep on the wing nearly as long as *echeria* ; moreover, it is much more wary, and always on the alert for danger, going off at a smart pace when frightened, and not returning to the same spot, as *echeria* frequently does, after being struck at ; altogether it is a much more difficult insect to capture. Indeed I do not see why the mimic should not somewhat surpass the mimicked species in numbers, without upsetting their relations to one another, provided the taste of the latter be sufficiently unpleasant, and particularly if the flavour be of a lasting nature.' This communication from so careful an observer as Mr. G. A. K. Marshall is not only exceptionally interesting, but shows the immense value of actual observation of the habits and natural surroundings of the insects themselves. Indeed it is not too much to say that

¹ The theory of reciprocal mimicry or Diaposematism has been criticized at some length by Marshall, for the details of which the reader may be referred to Trans. Ent. Soc., 1908, p. 93 et seq. The criticism affects, not the fact of Müllerian mimicry, but its relative importance, and I therefore feel that, so far as the present work is concerned, the discussion

may well be left in its present stage pending such additions to our practical knowledge of the subject as may reasonably be expected to accrue from further research.

² See Trans. Ent. Soc., 1902, p. 503.

³ *Hypolimnas dubius*, f. *mima*.

suggestions as to the mutual relations of living creatures should always be received with caution in the absence of precise data concerning the conditions under which they maintain their position in the struggle for existence.

Since the publication of Bates's original paper, many observations bearing on the subject have from time to time been communicated to the various learned societies and scientific journals. Wallace's paper in the Transactions of the Linnaean Society, 1866, vol. xxv, supplied numerous striking instances of mimicry from the Eastern Tropics, and Trimen dealt with the same phenomena in the Ethiopian region in his paper read before the same society in 1868. It is to this latter naturalist that we owe the discovery of one of the most curious and complicated instances of protective mimicry with which we are at present acquainted, namely, that of the polymorphic mimetic forms of *Papilio dardanus*. In 1882 Professor Raphael Meldola published a paper in the Annals and Magazine of Natural History in which he supports the theory of Müllerian mimicry, and shows how it may be made applicable even to the cases which have been observed of resemblance between butterflies of nearly related species. The question as to which is the model and which is the mimic does not, under such circumstances, require to be decided, since under the hypotheses already mentioned each species will benefit in a fixed proportion to the number of individuals.

It may be here noted that the phenomenon of mimicry in relation to sex presents many interesting peculiarities. In some cases the sexes of the mimic are similar and resemble one model. In others both model and mimic may be sexually dimorphic, when the corresponding sexes resemble each other. There are cases where the dimorphic sexes of a mimic resemble models of different species, whilst a non-mimetic male may have more than one form of female, each resembling a different model. It will be found, however, that in very many cases the female only is mimetic, the phenomenon being thus frequently associated with sexual dimorphism. This special development of mimicry in the female sex was originally explained by Wallace (loc. cit.) on the supposition that 'their slower flight, when laden with eggs, and their exposure to attack while in the act of depositing their eggs upon leaves, render it especially advantageous for them to have some additional protection'. An interesting discussion on this point will be found in Professor Poulton's essay on 'The Value of Colour in the Struggle for Life'.¹ It is there pointed out that while Wallace's hypothesis would in large measure account for the facts, it may be doubted whether it offers a complete explanation, and that amongst other considerations the greater colour variability of the female may have been an important factor in determining the predominance.

Consideration of other features of the subject will be found in the latter part of this volume. Batesian mimicry presents a comparatively simple aspect of the case, whilst mimicry between distasteful forms may be, and frequently is, of a highly complicated nature. As already pointed out, it is based on the inability of insectivorous foes to distinguish instinctively between edible and distasteful species. It has been asserted that young creatures do know what to touch and what to avoid, though such experiments as have been made have given results which are in favour of the contrary view. It has been pointed out that birds must know how to avoid poisonous berries, otherwise they would be destroyed by eating them. It seems questionable, however, whether many berries are in fact poisonous to birds. The formation of berries is a development which has been attained by plants for the better dissemination of the seeds which the berries contain and the object of the berries is to attract birds in order that the seeds may be eaten and distributed by the natural

¹ 'Darwin and Modern Science,' Essay XV, p. 292. Cambridge, 1909. (Reprinted in 'Darwin and The Origin,' Poulton. London, 1909.)

processes of digestion, which do not destroy the germinating principle of all the seeds ; and even if the previous assertion were proved, it seems impossible to understand how any animal can have inherited an instinctive knowledge of all the many and varied butterflies which are unfit for food, and it should be borne in mind that whilst a butterfly, or even a berry, may be distasteful, it need not be actually poisonous. Also it should not be forgotten that distastefulness is not an absolute property. There may be, and almost certainly are, wide differences between species in the degree of their distastefulness. Such differences might even account for Müllerian mimicry of a comparatively rare by a numerous species, provided the former were considerably more objectionable than the latter. These considerations, together with other interesting questions which arise, will be more conveniently appreciated after a closer acquaintance has been made with some of the instances of mimetic resemblance presently to be described. It will be seen that the subject of mimetic association in Lepidoptera falls under two heads of the table of animal coloration given above. Imitation of a distasteful species by a butterfly which is of an edible kind, the phenomenon known as Batesian mimicry, is a form of pseudaposematic coloration. The mimetic groups formed by the resemblance of two or more distasteful species (Müllerian mimicry) form a special case of aposematism, and the forms are spoken of as synaposematic.

Butterflies, then, form a large group of insects whose structure differs sufficiently to enable us to divide them into various families and genera. Although they are all butterflies, these differences from an anatomical point of view are great. Many butterflies, however, between which such differences occur, by a special modification of colour and form, superficially resemble each other so closely that they are only to be distinguished by a careful examination. These resemblances have been attributed to distasteful properties possessed by certain species, the appearance of the latter having come to be simulated either by other nauseous forms or by species which are in reality edible, the process of selection by insectivorous enemies having been the primary influence which, working on favourable variation, has caused the resemblances in question. Bearing these points in mind, we now pass on to consider instances of interspecific resemblance ; after which, we shall be in a better position to appreciate the theoretical considerations to which the subject gives rise. We shall find that as in other sections of the animal kingdom, so in butterflies, colours are seldom if ever the result of chance development, except in so far as they may be said to have been developed by selection from such variations of prior forms as have afforded their possessors some advantage in the struggle to continue their kind. Beautiful as are so many of the colours and patterns found in nature, it cannot be said, except perhaps in the case of epigamic colours, that beauty for its own sake has had anything to do with their formation. In Darwin's words, 'nature cares nothing for appearances except in so far as they are useful to any being.' Colour, though only a sensation perceptible to our senses, and not a phenomenon possessed of a material existence, is exhibited by all visible creatures, and is the property by which we distinguish their form and outward characteristics. The beautiful adaptations which we see around us are not the often quoted 'provisions of nature'. Nature's only provision is the tendency to vary. We see the survivals, but the inappropriate variations, which form the overwhelming majority, have been ruthlessly destroyed. They are extinct. The goal is perfection of adaptation, and the penalty for lack of success is destruction. The patterns of butterflies' wings, once regarded with merely interested admiration, have become, in fulfilment of Bates's foreshadowing, the pages on which we can read the past history of the everlasting conflict between the hunter and the hunted, and the complicated process by which new forms have adapted themselves to changed and changing circumstances.

I

DESCRIPTIONS OF MIMETIC ASSOCIATIONS IN AFRICAN RHOPALOCERA

DANAIDA CHRYSIPPUS.

Linnaeus, Syst. Nat., ed. 10, p. 471 (1758).	var. <i>albinus</i> , Lanz.
Cramer, Pap. Exot., pl. cxviii, ff. B, C (1777).	Klug, Symb. Phys., pl. 48 (1845).
Trimen, S. Af. Butt., i, p. 51 (1887).	Trimen, S. Af. Butt., p. 53 (1887).
Aurivillius, Rhop. Aeth., p. 32 (1898).	var. <i>alcippus</i> , Cramer.
var. <i>dorippus</i> , Klug.	Cramer, Pap. Exot. 2, p. 45, pl. cxxvii, ff. E, F (1777).
Klug, Symb. Phys., pl. 48 (1845).	Trimen, S. Af. Butt., p. 53 (1887).
Trimen, S. Af. Butt., p. 53 (1887).	var. <i>alcippoides</i> , Moore.
var. <i>albinus</i> , Lanz.	Moore, Proc. Zool. Soc., p. 238, pl. 31, f. 1, (1883).
Lanz, Iris, ix, p. 130 (1896).	

The butterfly which forms the central figure of our first mimetic association is one of the most interesting as well as one of the most widely distributed of exotic Lepidoptera. With the exception perhaps of the extraordinarily ubiquitous *Pyrameis cardui*,¹ *D. chrysippus* might fairly be described as the commonest butterfly in the world, so wide is its geographical distribution, and so great its numbers of individuals. It seems probable that the species can claim the respect due to venerable ancestry. In the British Museum there is a Theban fresco on which are depicted numerous figures of birds, fishes, and other natural objects, amongst these being seven representations of a butterfly, and though the details are somewhat obscured by the lapse of time, the pictures certainly bear a marked resemblance to this insect. The fresco is considered to be some 3,500 years old. The butterfly is common in Egypt to this day, and was described about a hundred and fifty years ago by Schreber as *Papilio aegyptius*.

D. chrysippus presents several well-marked and constant varieties. The typical form is represented on Plate II, Fig. 2, which shows both the upper- and underside of the female. The sexes are alike in pattern except for the presence in the male of the large black spot on the first median nervule in the hind-wing. The ground-colour in typical specimens varies from the bright golden-yellow of Fig. 2 to the darker red-brown of Fig. 1. Generally speaking it may be said that the dark form is characteristic of African specimens. Certainly it is comparatively uncommon in the Oriental region, and the large majority of those I have from Africa are of this colour. A very dark form (*cratippus*) occurs in Amboina and Ceram, but in this the markings are somewhat suffused, and the whole insect has a cloudy, smoky appearance. The first variety occurring in the African region is the *alcippus* form described

¹ My friend Dr. G. B. Longstaff tells an amusing story in this connexion. A friend remarked to him that he had no doubt that *P. cardui* would be found on the top of the Great Pyramid, and also that hibernating specimens would be discovered at the

North Pole. Dr. Longstaff replied that though he had not yet visited the latter region, he had once climbed to the top of the Great Pyramid, and that he did in fact on that occasion observe *P. cardui* hovering round the apex of that celebrated edifice.

by Cramer in 1777, Plate II, Fig. 3, which is characterized by having the yellow of the hind-wings largely replaced by white. The fore-wings of this variety are usually of the golden-yellow coloration, though I possess a single specimen from Entebbe which is of the darker form, and has the hind-wings nearly as white as in the example figured. Moore, in Proc. Zool. Soc., 1883, Part ii, described and figured a form which he named *alcippoides*. It differs from *alcippus* in that the fore-wing has a broader series of white sub-apical spots, and the white spot below these is much larger. There is a lower discal spot in the yellow area between the first and second median, and the hind-wings have somewhat less white than in *alcippus*. On Plate II, Fig. 7, is shown a variety which is without the black and white sub-apical bar in the fore-wings. This form is the *dorippus* of Klug. The general colour often has a tendency to be somewhat duller and paler than in the example shown. I have not seen this form having the dark brown ground-colour. Plate II, Fig. 9, shows the variety *albinus*. This resembles the *dorippus* form but has the hind-wings suffused with white, and bears the same relation to *dorippus* as *alcippus* does to *chrysippus*. Some confusion has occurred in recent works with regard to the nomenclature of these forms. Klug described *dorippus* and a white hind-winged form as a variety of it (the form now called *albinus*). In the Proc. Zool. Soc., 1885, part iv, when describing Lepidoptera of Somaliland, Butler, by an oversight, described the *dorippus* form as being unnamed and gave it the name *klugii*, and the name *dorippus* was given to the white hind-winged form¹. The mistake became emphasized by a paper read before the Bombay Natural History Society in 1892 by Colonel Yerbury, in which, presumably relying on Butler's description, he pointed out that *dorippus* bore the same relation to *klugii* as *alcippus* to the type form. It must be understood, therefore, that the name *klugii*, frequently found in entomological literature of recent years, refers to the original *dorippus* form described by Klug, and the white hind-winged form frequently called *dorippus* should be *albinus*. The *alcippus* described by Marshall and De Nicéville in their 'Butterflies of India' is probably equivalent to the *alcippoides* variety.

Trimen describes the larva as follows :—

'Pale bluish-grey; on the back transversely barred with bright pale yellow and streaked with white. Yellow bar in front of each segment from third to twelfth, (both inclusive), edged with black both anteriorly and posteriorly, and usually divided mesially by a short black streak uniting the black edges; three thin black streaks across each of these segments in its middle and posterior portion, and three similar streaks also on second and last segments. Front of head with a black horseshoe-shaped streak; spiracular stripe bright yellow rather suffused; legs bluish-grey barred with black. Three pairs of moderately long, black, flexible filaments springing from the back of the third, sixth, and twelfth segments respectively, in each case from near the extremities of the transverse yellow bar; all these filaments are crimson just at the base, and the first pair larger than the others. Length, 1 in. 6-9 lin.'

The pupa occurs in two forms and occasionally shows intermediate gradations. It is either green or pinkish and is ornamented with gold spots which disappear as the imago becomes developed therein. Wood-Mason, who has found by experiment that males and females are produced indifferently from the pink and yellow forms of the pupa, considers that the dichroic phenomena which it exhibits form an instance of cryptic colouring, the insect at this stage harmonizing either with the green leaves or the pink blossoms of the plant on which it is suspended. Trimen, however, does not think that the colour of the pupa is affected by its surroundings, he having allowed the larvae in confinement free choice

¹ There was a certain amount of excuse for this error, since in the plate accompanying Klug's description the names are unfortunately reversed and *dorippus* is applied to the white hind-winged form.

of various convenient surfaces for pupation, but without direct result. As will be gathered from the description of the pupa, it is a very conspicuous object, and it may be concluded that the coloration is, in this stage, as in the perfect insect, aposematic. This remark applies as well, if not better, to the larva.

Messrs. Marshall and De Nicéville, already referred to, describe the three different forms of *chrysippus* as three species, though there is now no doubt that they are merely varieties. Col. Yerbury (loc. cit.) says, 'I have lumped these four forms together, as, however good species they may be elsewhere, at Aden they are only varieties. I have taken them *in coitu* in every possible combination, and have reared a considerable number of caterpillars, with the result of having obtained *L. chrysippus*, intergrades to *alcippus*, *dorippus*, and *klugii*. I could not detect the slightest difference between the larvae that produced these different results. The pupae are dichroic, green and light purple, and are very beautiful, looking as though they had been carved out of the wax tapers used to decorate Christmas-trees.' Also in the same author's notes on this species mentioned by Butler in Proc. Zool. Soc., 1884, part iv: 'I have taken *dorippus* and *chrysippus* *in coitu* so often that I have given up catching them as a curiosity.'

Butler says that from notes attached to the specimens it would appear that the green chrysalis produced *klugii* (*dorippus*), and the purple form *chrysippus* with intergrades towards *alcippus*.

As regards the geographical distribution of *D. chrysippus*, the type form may be said to extend from Southern Europe to the Cape, and from the Canary Islands to Eastern Asia. The *dorippus* form does not occur in Mauritius, is comparatively rare in South Africa, and is not found in West Africa. In a collection made by Dr. Wiggins on the Victoria Nyanza, *dorippus* was the dominating form with 163 individuals against 136 of the type. There were in all 342 examples, and *alcippus*, *alcippoides*, and *albinus* occurred in the numbers of 18, 16, and 13 respectively. A collection made by Mr. Byatt on the Nyassa-Tanganyika plateau, contained, on the other hand, 288 typical *chrysippus* and only 8 *dorippus*. Mr. Lathy, in Trans. Ent. Soc., 1903, p. 184, states that *alcippus* was the prevalent form in a collection from Anambara Creek on the river Niger in West Africa. In the same volume Dr. Dixey described a collection made by Mr. W. L. S. Loat on the White Nile, and in this region all the varieties occurred together in the same manner in which Col. Yerbury describes them as occurring at Aden. Lieut.-Col. Manders (Trans. Ent. Soc.) records the occurrence of the type form in Bourbon and Mauritius. Generally speaking *alcippus* may be said to be commonest on the west coast, and *dorippus* on the east.

As Col. Yerbury had studied the forms of this butterfly in so favourable a place as Aden, I wrote to him for any facts of interest which he might be able to furnish, and he very kindly replied, giving me his views on the meaning of the different forms. The portion of his letter dealing with the subject is as follows: '*Danaïs chrysippus* in its tetramorphic form appears to have been first established in the countries round the Gulf of Aden (Aden to the White Nile). This tetramorphic form is the ancestral form and has spread from the centre in all directions, the form best suited to its environment being that which has established itself in any particular locality, the other forms only appearing as cases of reversion under unusual circumstances. As regards the four forms of the butterfly, I would divide them into two groups, which I will call the primary and secondary forms of this species. The primary group consists of *chrysippus* and *klugii* (*dorippus*) and these two forms are determined at an early stage by the following conditions. Should the weather be normal after the hatching of the egg, everything will be favourable for the appearance

of *chrysippus*. Should the weather become dry, or a drought set in, and the larva possibly have to aestivate, then the conditions will be favourable to the appearance of *klugii* (*dorippus*); though I consider that *chrysippus* will always prove to be the predominant form, and that even under the most favourable conditions *klugii* (*dorippus*) will never surpass, perhaps never even equal it in numbers. The white on the hind-wing of the secondary group, *alcippus* and *dorippus* (*albinus*), I look on as the brand of humidity affecting the butterfly while in the pupa stage at a most susceptible stage of its existence. The pupa skin has, I believe, been compared to a photographic plate, and possibly this white blaze may be due to the reflection of the sun's beams from the drops of water, and may be similar to an attempt to photograph the roof of a conservatory with the sun shining on it. When one considers the extremely local and partial distribution of the rainfall in desert and semi-desert countries, there seems nothing improbable in the four forms of *D. chrysippus* being evolved close together in a restricted area. The argument in support of local races that *alcippus* alone occurs on the west coast of Africa (Sierra Leone, &c.) appears to me to be of little value, the driest season in that district being in excess of the wettest round the Gulf of Aden. If, however, it can be shown that *alcippus* alone occurs in the drier regions of French Senegambia inland from Dakar and St. Louis, the argument will become much stronger, for here I should expect the tetramorphic form to exist, the exact form appearing to be dependent on local conditions.

'With reference to the distribution of *chrysippus* the occurrence of the *klugii* (*dorippus*) form near Trincomali is of interest, the Foul Point district being the driest in the island.'

This letter was written some time ago, and before there was so large an amount of material to work upon in connexion with this species. An interesting discussion on the origin of the forms of *D. chrysippus* was communicated to the Entomological Society in 1902 by Professor Poulton, and the conclusions differ so much from those of Col. Yerbury that it is desirable here to recapitulate them. Mr. and Mrs. S. L. Hinde captured a set of fifteen specimens on May 6, 1900, almost on the sea level in the uniform damp heat of Mombasa. Of these four were of the type form *chrysippus* and eleven of the *dorippus* variety. All were taken in less than an hour in a spot of ground a few yards in extent, thus affording a fair criterion of the proportionate numbers of the two forms. The second set of about thirteen was taken at a height of about 5,400 feet at Machakos Road on the Uganda railway on May 22, 1900, and consists of four of the type form, one *alcippoides*, and seven *dorippus* and one *albinus*. These were also taken in a spot of ground a few yards in extent in less than an hour. May 22 was at the end of a very dry wet-season in an exceptionally dry year. The specimens show the effect of this, being on the average much smaller than those bred from larvae, which fed on the more luxuriant food plant in Mombasa. An examination of the two series favours the conclusion that the Machakos larvae were partially starved, probably feeding on a parched food plant. It is further shown that a comparison of the two series indicates very strongly that the various forms of the species are not in any way due to environmental causes, but are inherent and hereditary. '*Dorippus* is considered to be due to drought, but there is a larger proportion of this form in the series bred in the moist heat of Mombasa than in that reared at high and dry Machakos. The great difference in conditions which is manifest in the different average size of the two series was powerless to effect any change in the inherent hereditary tendency of the individuals to become either *klugii* (*dorippus*) or its modification *dorippus* (white form), the type form, or its modification *alcippoides*.'

This comparison of forms from adjacent localities under different climatic conditions

leads to an inference which is precisely the same as that drawn from the comparison of forms from different localities under the same climatic conditions. The tropical forests of West Africa and the Malayan Islands are very similar as regards climate ; in the first *chrysippus* occurs as the white hind-winged *alcippus*, in the second as the type form, a peculiar dark form inhabiting Java.

Having thus thrown some doubt on the influence of climatic conditions, the author proceeds to account for them by the all-pervading influence, natural selection. He suggests that the *klugii* (*dorippus*) form is a development in a procryptic direction in areas where the struggle for existence is so severe that even the unpalatability of the species is an insufficient protection against enemies goaded to hunger by the scarcity of insect prey. In support of this assumption it is pointed out that the ground-colour of *dorippus* is modified in some specimens to a decided sand-colour, such modification being more noticeable in Africa where the type form is usually of the dark golden-brown colour already described as typical of the African region. Such a view implies the assumption that *dorippus* has developed from *chrysippus* and not *chrysippus* from *dorippus*, in support of which Professor Poulton continues as follows : ' Island individuals which are so generally ancestral are *chrysippus*, and only very rarely *klugii* (*dorippus*), except near the metropolis of the latter form in Somaliland. Perfect and imperfect mimics, Batesian and Müllerian, are very large in number, especially in Africa. Probably not one of these mimics *klugii* (*dorippus*) and not *chrysippus*, a few mimic both, while the great majority mimic *chrysippus* alone. Again *klugii* (*dorippus*) stands alone among *Danainae*, while the pattern of *chrysippus* is closely related to that of several other species and genera, such as *Salatura*. The distribution of *klugii* (*dorippus*) can be understood by supposing the desert region of Somaliland to be its centre. From this point it radiates towards the east, becoming gradually rarer, although it is well known in Karachi, and Col. Yerbury even captured a single specimen in Ceylon ; towards the south, finally disappearing in South Africa ; towards the Nile Valley, here also probably disappearing towards Central Africa. *D. chrysippus*, or at least forms with a black and white apex to the fore-wings, on the other hand, occur over the whole vast range of the species, with the exception of certain parts of Somaliland.'

Further and still stronger arguments are deduced from consideration of some of the forms of mimicking species. Marshall considers the form *alcippus* to be a further development in the direction of still more efficient warning colours, in which view Professor Poulton concurs, in view of the abundant life of Tropical West Africa, and of the fact that it is much more conspicuous on the wing.

Were *alcippus* to occur only in Tropical West Africa the views of the origin of the various forms of *D. chrysippus* just explained would no doubt be much strengthened, but as Marshall has pointed out, this form presents some difficulties, occurring as it does at Aden, Wadelai, &c., and is also common on the Tugela River. Further difficulty is presented by the *albinus* form, for if the coloration of *dorippus* is procryptic and that of *alcippus* aposematic, we have in *albinus* the simultaneous development of two features of opposing significance. There is a general tendency to a more or less white suffusion, especially of the hind-wings, in *chrysippus*, for many specimens from various localities exhibit it in a greater or less degree. It would, therefore, seem reasonable to suppose that this tendency is inherent in the species, and is not inhibited by the development of the other variations. If this were so, the white hind-wings would become general wherever the conditions of life favoured them more than the other forms, as for instance appears to be the case, from whatever cause, in West Africa. In other localities there might be no special advantage in white hind-wings over the typical

yellow, and here we should have both forms occurring, the yellow or dominant form being most numerous. Such a view of the appearance of the white suffusion would in some measure reconcile the views of the authors quoted, *albinus* being regarded as an occasional reversion to the white suffusion, which tendency the modification of *chrysippus* to *dorippus* has not entirely eliminated. The comparative rarity of *albinus* seems to support this view. Though we are as yet very imperfectly acquainted with the natural causes which determine the transition of white to yellow or vice versa in the colours of Lepidoptera, such a variation would seem to be fairly common. Other species, as for instance *Amauris echeria*, occur either as yellow or white spotted forms without any very obvious reason for the variation. In the paper on the chemical nature of lepidopterous pigments by Professor F. Gowland Hopkins, already quoted, it is pointed out that in the group *Pieridae* an important point is the interchangeability between white, yellow, and orange, as shown by the colouring of closely allied species, and even in variations of the same sex and species. These remarks apply, it is true, to the *Pieridae*, to which group the forms now being considered do not belong, and in which the pigments appear to be of a different constitution to those of other families. They supply, however, another instance of the variation from yellow to white, and, what is still more interesting to note, Professor Hopkins is of opinion that the white colour is due to oxidation of the yellow taking place in the pupal condition, a suggestion which reminds us again of Col. Yerbury's theory as to the origin of the white suffusion. There are, however, many difficulties in the way of this latter proposition. *Alcippus* occurs principally on the west coast of Africa, and unless it can be proved that the climatic conditions there obtaining tend to produce oxidation more than those of other localities, there is little to support the explanation. There is also another and greater difficulty. If the white hind-wing is the product of the actinic effect of light on the pupa, why is not the fore-wing affected, since in the pupal state it lies over the other, and should therefore be the first to be acted upon?

It will be seen from the foregoing considerations that much still remains to be discovered respecting the origin of these different forms. They are not due to the phenomenon known as seasonal dimorphism, and there are difficulties in the theory of climatic conditions, since in some localities the different forms occur together. We can, therefore, only conclude that the species is of a somewhat unstable nature, liable to vary approximately on the lines of the three principal varieties, and that natural selection has caused these three varieties to become somewhat pronounced and fairly constant in some localities. Given that a species is liable to variation, natural selection will guide such variation along the lines most calculated to perpetuate the species. If the tendency to variation is slight, the original pattern and colour may be altered in course of time, but there will not be a great liability to form well-marked contemporary varieties. If, on the other hand, the species is of an unstable nature and the liability to variation great, there will be greater and more frequent opportunities for natural selection to form well-marked varieties which can fill a new place in the economy of nature. The very evident adaptability of *D. chrysippus* to varied circumstances is evidenced by its extraordinarily wide geographical distribution, and whilst all forms may occur together in certain localities, the predominant form will be that best suited to the immediate circumstances. Such circumstances are undoubtedly exceedingly complicated. Whilst one insect may be modified so as to escape its enemies solely by its resemblance to a protected species, the latter in turn will be altered to suit other conditions which in the light of our present knowledge are too obscure to be fully understood. Apart, however, from the special advantages enjoyed by the different forms of *D. chry-*

sippus, collectors are generally agreed that the insect is beyond question extremely distasteful to insectivorous animals. The larvae are very conspicuous, and, as Leigh has pointed out (Proc. Ent. Soc., 1903, p. 22), they employ no disguise, and are certainly unpalatable and avoided by birds, hornets, spiders, and *Mantidae*. The pupae are equally devoid of cryptic protection, and the perfect insects are slow flying and careless of pursuit. Even dead specimens in the cabinet are said to be less prone to the attacks of mites than are other species. Wherein lies their nauseous quality it is exceedingly difficult to discover, but there is no doubt that they have a disagreeable smell. Dr. Dixey, in Proc. Ent. Soc., 1906, says: 'The scent in both sexes of *chrysippus* invariably appeared to me to be of a strong and disagreeable nature, like that of cockroaches, often stronger in the females. . . . The excised glands of the male yield on pressure a yellow or brown juice, without perceptible taste or odour.' Again, in Trans. Ent. Soc., 1905, p. 104, Dr. Longstaff remarks: 'Here I observed in two specimens of *chrysippus* (of which certainly one was a male) a distinct cockroach-like odour, sufficiently strong to be perceptible when the insect was fluttering in the net.' Again (p. 108): 'Here I one day had the advantage of the assistance of my host, Mr. Edwin Scott, I.C.S., whose keen appreciation of scents helped me greatly. *L. chrysippus* was abundant; of its scent Mr. Scott's first impression was "some sort of dung", then, "a zoo"; later he said, "possibly like a cockroach but more like a musk rat." The scent is, I think, general, but is perhaps stronger when the scent sacs in the hind-wing are opened: a fact that I also observed at Calcutta.'

In *chrysippus* we have therefore a conspicuous butterfly of exceedingly wide range, producing several well-marked and constant varieties, and by its habits, abundance, and carelessness of pursuit, furnishing ample evidence of its distasteful qualities. It remains to consider the species which are mimetically associated with it.

HYPOLIMNAS MISIPPUS.

Linnaeus, Mus. L. Ulr., p. 264 (1764).
 Godart (*misippe*), Enc. Meth., ix, p. 188 (1819).
 Cramer (*diocippus*), Pap. Exot., i, pl. 28 ff. B, C (1775).
 Drury (*bolina*) Ill. Ex. Ins. p. 26, pl. 14, ff. 1, 2 (1773).
 Trimen, S. Af. Butt., i, p. 277 (1887).
 Aurivillius, Rhop. Aeth., p. 147 (Synonymy) (1898).

var. ♀ *alcippoides*, Butler.
 Butler, An. N. H., v, xii, p. 102 (1883).
 Trimen, S. Af. Butt., iii, p. 404 (1889).
 var. ♀ *inaria*, Cramer.
 Cramer, Pap. Exot., iii, p. 36, pl. 214, f. A, B (1779).
 Trimen, S. Af. Butt., i, p. 278 (1887).
 var. ♀ *dorippoides*, Aurivillius.
 Aurivillius, Rhop. Aeth., p. 148 (1898).

The resemblance of the female *H. misippus* to both sexes of *D. chrysippus* is probably the best-known instance of mimicry in butterflies. The species was described in 1776 by Sulzer as the female of *D. chrysippus*. It presents a striking instance of the phenomenon of sexual dimorphism, the male and female being entirely different in appearance. As will be seen later this phenomenon is by no means an uncommon one, especially in butterflies which exhibit mimetic resemblance. Further than this the species also exhibits the extraordinary feature of female polymorphism, i.e. the female occurs in several different forms, and though in this case the forms resemble the varieties of one species of model, we shall find that there are butterflies the females of which present several different appearances, each resembling a specifically distinct model.

The typical form of the female is illustrated on Plate II, Fig. 8, from which the general resemblance to *D. chrysippus* can be clearly seen. The male is shown on the same plate, Fig. 5. The difference in the appearance of the two sexes is so great that it is at first very

difficult to understand how such a great modification can have been brought about, assuming that the male represents the ancestral coloration. In this case we see, however, the completed condition without the intermediate varieties, and further acquaintance with mimetic forms will disclose instances in which the progress of the development of the mimetic pattern can be more easily traced. It should be borne in mind that we are not bound to suppose that the insect which acts as a model should not at one time have borne characters which enabled an easier approach on the part of the mimic. Further than this, we owe to Dr. Dixey¹ the knowledge that a mimetic butterfly need not necessarily have begun its course of mimetic modification in association with the species which now forms its model. This author has shown how in certain cases amongst the Neotropical butterflies a very small variation in the pattern of a butterfly may bring about a useful resemblance to some other species. This change having been established, a further slight modification may cause the insect to enter the sphere of attraction of some other dominant form, and this process repeated may culminate in the ultimate form exhibiting very wide differences from its ancestral type, differences which appear inexplicable when the intermediate and connecting links have been removed. In the case of *H. misippus*, we are not, however, entirely without knowledge of an intermediate form. The Oriental *H. bolina*, the male of which is very similar in appearance to *H. misippus*, has a form of female known as *nerina*, which shows a reddish-brown suffusion of the wings which would appear to hint at the origin of the present colour of the female *H. misippus*. The present typical form having been established, only a small step is necessary to produce the remarkable variations shown on Plate II, Fig. 6, which shows an example of the variety *alcippoides*. Here we have a white suffusion of the hind-wings causing the insect to resemble the *alcippus* variety of *chrysippus*. Fig. 10 shows the form *inaria* which is losing the black and white apical area in the fore-wings in correspondence with *chrysippus dorippus*. Occasionally, as in Fig. 4, *misippus* is of an unusually dark form, thus resembling still more closely the usually dark examples of its model in the African region. The *inaria* form sometimes develops a tendency to albinism in the hind-wings forming the variety *dorippoides*, Fig. 12, thus approaching *chrysippus albinus*, whilst intermediate forms are occasionally found, such as that shown in Fig. 16. It is interesting to note that from a female very similar in appearance to Fig. 16, Mr. Rogers at Rabai bred fifty females of *misippus*, all of which were of the *inaria* form, the sole variation being that some had a tendency to albinism in the hind-wing. It is one of these examples which I have shown at Fig. 12.

As with *D. chrysippus*, the geographical range of *H. misippus* is exceedingly wide, in fact it is actually found in regions where the former insect does not occur, as for instance in Florida and in South America. The only Old World locality in which it does not, so far as has been recorded, accompany its model, is on the European shore of the Mediterranean. Dr. Longstaff found a single damaged example of the male of this species in the Khedivial Agricultural Society's Museum at Cairo. The specimen had been taken in the district, an interesting fact which shows the extreme range of the species to extend further north than is generally supposed. Collectors agree that the similarity between the two insects when alive is such as to deceive even a practised eye. This is not to be wondered at when it is known that even the male *D. chrysippus* is deceived. Trimen describes how he once watched a male of the latter species pursue for a long time a female *H. misippus*, in the belief that it was one of its own species. Dr. Longstaff also records (Trans. Ent. Soc., 1905,

¹ See Mimetic Attraction : Dixey, Trans. Ent. Soc., 1897, p. 317, &c.

p. 109) that when at Anatapur (India) he several times saw the male *misippus* pursuing *chrysippus* as though under the impression that it was a female of its own species. Marshall (Trans. Ent. Soc., 1902, p. 480) says, 'I certainly think that I have more frequently seen *H. misippus* (female) in company with *L. chrysippus* than with its own male. The latter is fond of haunting the tops of kopjes in company with various species of *Precis* (which always occur in such localities), but I have never seen the female do so, neither does *chrysippus*.

Trimen thus describes the larva and pupa.¹

'Larva. Fuscous brown on back; sides dull greenish, with two longitudinal dull red streaks (of which the upper one is broader); all the legs red. Head dull red, with two rather long, divergent, spinose, black horns. Body beset throughout with blackish branched spines, tinged with pale red at their bases. Feeds on *Portulaca oleracea* and *P. quadrifida* (M. E. Barber).

'Pupa. Brownish yellow-ochreous, varied with very dark brown; abdominal segments rather closely ringed with fine fuscous parallel lines; back of thorax irregularly patched with very dark brown; wing covers all dark brown, except for some ochreous spotting near extremity.'

H. misippus seems to have a great tendency to become widely spread over great distances. It is very strong on the wing, and though when undisturbed the female flies slowly in a manner imitative of its model, it becomes very wary when pursued and never returns to the same spot. The ability of this insect to travel great distances, even over the sea, has been illustrated in a most interesting manner by Professor Poulton's account of a swarm of these butterflies having been met by the sailing ship *Winifred* when over 500 miles from land.² Captain E. P. Ellis, of the ship referred to, forwarded three females and two males, two of the former being of the *inaria* variety. Captain Ellis's notes as given by Professor Poulton are as follows:—

'May 5, 1893. In 00 36' N. lat. and 26° 42' W. long., a swarm of butterflies about the ship; they appear to be all of one kind.'

'May 9, 1893. In 3° 56' N. lat. and 27° 20' W. long. Butterflies all over the ship; the sailors knocking them down with their caps from one end of the ship to the other.'

The further particulars and comments are best given in Professor Poulton's own words. 'Captain Ellis also informs me that during these days the ship had passed through the region of the doldrums with calms and rain squalls between the north-east and south-east trade winds. To the best of Captain Ellis's recollection and opinion all the butterflies belonged to one swarm and were of the same kind on both occasions. The ship was then nearly on the line between Cape St. Roque and Sierra Leone, and 580 miles from the former, 960 miles from the latter. Although the African coast was far more distant than the South American, I cannot doubt that the insects came from the former. Indeed, I put down Tropical West Africa as first among the suggestions thrown out in my note (vol. xii, p. 80). The only other possibility is Tropical South America, a country in which *H. misippus* has comparatively recently established itself and is spreading rapidly. The insufficient observations that have been made in South America do not justify the belief that the *inaria* form of the female is present in large proportion, while two out of the three females captured at sea belonged to this variety—a proportion entirely consistent with our much more extensive series of observations upon this species in West Africa. Furthermore, the species is not sufficiently abundant in South America to render it probable that these vast swarms can have come

¹ S. Af. Butt., i, p. 279. (*Pupa* figured, pl. 1, f. 5.)

² 'Entomologist's Record,' vol. xii, No. 11, Nov. 15, 1900.

from there. The observation throws much light upon the comparatively recent intrusion of the species into South America, and its even later spread to the Canary Islands, and goes far to explain its extraordinarily wide distribution in the Old World.'

H. misippus presents a certain amount of difficulty when viewed as an instance of mimicry, inasmuch as the geographical distribution of its varieties presents a noticeable lack of coincidence with that of the varieties of *D. chrysippus*. Thus the *inaria* form of *misippus* is commoner in South Africa than the type, while the *dorippus* form of *chrysippus* is rare. In West Africa the *alcippus* form of *chrysippus* is predominant, whilst here the *inaria* form of *misippus* is common. In British East Africa there is a better correspondence, but on the whole the varieties of the two species do not appear to show any well-marked coincidence. Those who are opposed to the theory of mimicry, and who consider that the resemblance between butterflies of different genera is merely accidental, may consider the present case as strongly corroborative of their views. A little consideration, however, will show that this is not the case. In the absence of much needed experiment we must argue from probabilities. We have then the following facts. A butterfly, the ancestral appearance of which, as shown by the male and its allied species, is black with conspicuous white markings, shows in the female an entire departure from the family facies, and becomes practically indistinguishable, on the wing at least, from a widely distributed and apparently protected species of an entirely different genus. Such a phenomenon alone could not be accidental, but the resemblance goes much further. The model presents no less than three well-marked varieties, each of which is faithfully copied by a corresponding form of the mimic, and it would be straining a point to argue, because we are ignorant of the causes which have since led to the present geographical distribution of the varieties, that therefore the extraordinary resemblance between them is merely accidental. *D. chrysippus* is accompanied throughout its range by *H. misippus*, and although the latter is a recent arrival in America where the former is unknown, there may be different natural conditions in that country which combined with its migratory habits have enabled it to become established. Even if we were to assume the highly improbable hypothesis of accidental resemblance between the two forms, we must still find some explanation of the fact that *D. chrysippus* is more or less accurately imitated in outward appearance by a considerable number of other widely different species of butterflies which will shortly be described. It may be argued that a tendency to albinism is common in many butterflies, and that, therefore, the coexistence of *chrysippus alcippus* and *misippus alcippoides* can be explained on the ground that the albinistic tendency has produced in this case a kind of parallel variation. The extreme improbability of two species arriving at the same result by a process of parallel variation is pointed out in a later portion of this work. But if it were shown that a tendency to albinism exists in *H. misippus*, then that tendency merely becomes the material out of which a mimetic resemblance has been fashioned. Granted that *H. misippus* has produced its various forms in imitation of *D. chrysippus*, its wide distribution still, however, demands some explanation. Such an explanation is rather difficult to find if the species be regarded purely as a Batesian mimic, but there is considerable doubt as to whether it can be so regarded. Most species which are really palatable to insect enemies and depend for their existence on resemblance to protected forms are comparatively rare. They occur in isolated instances amongst swarms of their unpalatable models. *H. misippus* is a notable exception. It has established itself in America, where its model is unknown. The wide range of the insect may be due in some part to the abundance of its model, but the ease with which it appears to maintain large numbers of individuals points to the possession of at least some degree of unpalatability.

Professor Poulton has suggested that the case is one of Müllerian rather than Batesian mimicry.¹ Unpalatability is essentially a relative rather than an absolute quality, and it is easy to suppose that a species of slightly distasteful properties may strengthen its position in the struggle for existence by resemblance to a still more distasteful kind.

In Africa *H. misippus* is a very wary and active insect on the wing, especially when alarmed. It would be of great interest to learn whether in America it has adopted the habitually slow flight characteristic of very distasteful species.

It occurs over practically the whole of the Ethiopian region, portions of South and Southern North America, and the greater part of the Oriental region, extending to North-West Australia and Queensland.

PSEUDACRAEA POGGEI.

Dewitz, Nov. Act. Nat. Cur. (41), ii, p. 197, pl. 2, f. 2 (1879).

Trimen, Proc. Zool. Soc., p. 79 (1891).

Butler, Trans. Ent. Soc., p. 202, pl. 10, ff. 2, 2a (1892).

Aurivillius (Synonymy), Rhop. Aeth., p. 175 (1898).

Plate II, Fig. 11.

As the name of this genus implies, many of its members bear a resemblance to the *Acraeinae*. Indeed, the species of this genus may be said to exist for the most part by virtue of their false colours, since with the exception of one or two forms they are all imitative in both sexes of various protected species. To such a degree is this mimicry carried that in many cases experienced collectors have been deceived, the models and their counterfeits having been placed together in collections. *P. poggei* was described and figured by Dewitz in 1879 as a species of *Diadema* (*Hypolimnias*).² Both sexes of the species are represented in my own collection by examples from Johnstone Falls in North-East Rhodesia, and the female is figured on Plate II. The male differs very little from the figure, though it is rather smaller and its fore-wings are not so prolonged. Mr. Neave, who has had great experience of collecting in Tropical Africa, considers this species to be by far the most perfect mimic of *D. chrysippus* which has yet been discovered. He describes it as quite indistinguishable from its model when on the wing, a fact which may account for the comparative rarity of the species in collections since it is not really rare in the localities where it occurs. Until comparatively recently not a single example of this butterfly existed in the National Collection. Between October, 1898, and January, 1899, a collection of butterflies was made by native collectors under the direction of Père Guillème at Kayambi in North-East Rhodesia on the Chambezi River, and the specimens some seven years later were given to Mr. Byatt, who presented them to the Hope Department at Oxford. The same collector communicated a short paper on the subject to the Entomological Society in April, 1905. In it he describes how, with a total of 367 typical *chrysippus*, there were found seventeen examples of *Pseudacraea poggei*, representing a proportion of mimic to model of only $4\frac{1}{2}$ per cent., and even this being a much larger proportion than was formerly supposed; the author expressed the opinion that the mimicry appeared to be Müllerian rather than Batesian. At the February, 1908, meeting of the Entomological Society, Professor Poulton read a letter from Mr. Neave, who was then collecting in the Congo Free State. The writer there says,

¹ Proc. Amer. Assoc. Ad. Sci., p. 242, 1897. The argument is further extended in the same author's essay, 'Thomas Henry Huxley and the Theory of Natural Selection,' 'Essay on Evolution.' Oxford, 1908.

² In the reference given above Trimen pointed out the true affinity of this butterfly, assigning it to

the genus *Pseudacraea*, instead of to *Hypolimnias*, in which it had been included by Dewitz. The same author also pointed out the imitation of *chrysippus* as being even more perfect than that of the female *misippus*. The example then described was taken at Omrora, Ambuella Country, Angola.

'*Mimacraea marshalli*, Trim., and *Pseudacraea poggei* were just beginning to reappear at the end of October, and I have taken one of each. . . . I still think *P. poggei* the best mimic of *Danaida (Limnas) chrysippus*, even better than *misippus*—its flight is so extraordinarily like that of its model. It is rather, I think, a significant fact that of all the *Pseudacraeas* I have met with (5 spp.), *poggei* is by far the most abundant; while it is bold and not afraid to expose itself on the wing.' Mr. Neave has since told me that the species is by no means rare where it occurs. On one occasion he noticed a specimen of *chrysippus* and one of *poggei* behaving in a manner that suggested that one of the insects certainly mistook the other for an individual of its own species.

The example described by Butler came from Angola and is in the Tring museum. Mr. Trimen informs me that there is a female in the collection of Mr. Hobley which was taken in German East Africa. In order to be quite certain of the locality of the Tring specimen I wrote to Dr. Jordan on the subject, and he very kindly replied that the locality was quite correct, so that we evidently have a very wide range for this insect.

ACRAEA ENCEDON.

Linnaeus, Syst. Nat., ed. 10, p. 488 (1758).
 Linnaeus (*encedonia*), Syst. Nat., ed. 12, p. 762 (1767).
 Boisduval (*sganzini*), Voy. Deleg., ii, p. 590 (1847).
 Doubleday and Hewitson (*fulva*), Gen. D. Lep., p. 140, pl. 19, f. 2 (1848).
 Wallengren (*lycia*), Rhop. Caff., p. 22 (1857).
 Staudinger (ab. *infuscata*), Exot. Schmet., i, p. 83 (1885).
 Aurivillius (ab. *alcippina*), Rhop. Aeth., p. 111 (1898).
 Boisduval (ab. *sganzini*), Faune. Madag., p. 34, pl. 6, f. 6, 7 (1833).

Fabricius (ab. *lycia*), Syst. Ent., p. 464 (1775).
 Staudinger (*braunei*), Exot. Schmet., i, pl. 33 (1885).
 Hewitson (ab. *necoda*), Exot. Butt. Acraea, pl. 2, f. 9 (1861).
 Godman and Salvin (ab. *daira*), Proc. Zool. Soc., p. 221, pl. 17, f. 3 (1884).
 Trimen (*encedon* ab. ?), S. Af. Butt., i, p. 165 (1887).
 Vuillot (*usagarae*), An. E. Fr., 60 Bull., p. 78 (1891).
 Butler (*caecilia*), Proc. Zool. Soc., p. 566 (1894).
 Aurivillius (Synonymy), Rhop. Aeth., p. 110 (1898).

Plate III, Figs. 1, 2, 3. VIII. Fig. 16.

The genus *Acraea* is one which provides models for many mimetic butterflies in the African region, though in some cases the species are apparently drawn away into mimetic association with other dominant forms. They fly slowly, without any regard for concealment, and though gregarious in habit seem to be of quarrelsome disposition, and Mr. Trimen describes how two females of *Acraea horta*, observed by Mrs. Barber, struggled for a long time over the possession of a particular leaf of the food plant and ended by laying their eggs on each other and flying away with them. They are for the most part of a very conspicuous appearance, and the abundance of individuals, slow flight, and disregard for concealment point strongly to the possession, by most species at least, of properties which protect them from insectivorous enemies. They possess an offensive odour, which appears to be caused by a yellow fluid which is exuded from the thorax when the insects are handled.

Acraea encedon is most remarkable in having developed three principal varieties which correspond to varieties of *D. chrysippus*, in the same way as do the forms of *H. misippus*. In the typical form, Plate III, Fig. 1, the mimicry is that of the type form of *D. chrysippus*. The specimen I have illustrated is of medium size, but many examples are much larger, presenting a correspondingly closer resemblance to the model. The mimetic nature of the pattern was first pointed out by Professor Poulton at a meeting of the British Association

at Toronto in 1897, and in that year Marshall captured in South Africa several groups of butterflies which included these insects, together with *H. misippus* and other mimetic forms. The variety *daira* shown at Fig. 2 is distinguished by having lost the black and white markings of the apices of the fore-wings, thus producing an exact parallel with the *inaria* variety of *H. misippus* in mimicry of *D. chrysippus dorippus*, whilst in the white hind-winged form *alcippina*, the variety corresponds to *misippus alcippoides* and *chrysippus alcippus*. In view of the highly distasteful properties of the genus *Acraea* in general, the inclusion of *A. encedon* in the *chrysippus* association must be explained on the Müllerian hypothesis. The fact that it has been able to depart from the usual *Acraeinae* facies and adopt the aposematic pattern of another species is probably accounted for by the innate variability which, though a common quality of the members of its genus, is perhaps more than ordinarily developed in this species. Intermediate varieties are met with, but Professor Aurivillius gives the following list of forms which have been specially differentiated :—

1. *encedon*. The type as shown at Fig. 1.
2. *infuscata*, Staud. Similar to *encedon*, but the brown areas of a darker 'smoky' appearance.
3. *alcippina*, Auriv. The white hind-winged form, Plate III, Fig. 3.
4. *sganzini*, Boisd. The typical Madagascar form, though also occurring in South and East Africa. The brown areas are replaced by yellow.
5. *lycia*, Fabr. An albino form in which the brown areas are replaced by white.
6. *necoda*, Hew. The Abyssinian form in which the brown colour is replaced by grey, and the apical black of the fore-wings is wanting.
7. *daira*, Godm. and Salv. The form shown on Plate III, Fig. 2.

An examination of these forms shows that *infuscata* is merely a melanic form of the type and *lycia* an albino form. The *necoda* of Hewitson, judging from his figure, is an intermediate between *lycia* and *infuscata*.

On Plate VIII, Fig. 16, is shown an interesting form of *A. encedon*, in which the ground-colour is of a more golden tint than usual, whilst the sub-apical bar in the fore-wings is suffused with scales of the same rich yellow. The variety is very unusual, and was taken at Nyangori on the north-east shore of Lake Victoria Nyanza, in company with *Planema tellus* and *Acraea jodutta*. Should more examples of this variety be received, it will be reasonable to conclude that *A. encedon* is developing a form in mimetic relation with *Planema tellus*, a dominant model which with its other known mimics is described later.

In geographical distribution *A. encedon* and its varieties show a far more perfect coincidence with the forms of the model than do the varieties of *H. misippus*. The *daira* form is rare in South Africa, where *dorippus* is almost absent, and it becomes commoner as we pass northwards, where *dorippus* is also more numerous. Whilst all forms occur on the west coast, *alcippina* is more frequently met with there than elsewhere, and from some parts of the west coast specially large examples of *alcippina* have been received. The form *lycia* has been considered to be a development in the direction of *Acraea esebria*. Marshall in writing to Professor Poulton in 1896 (Trans. Ent. Soc., 1902, p. 479), says, 'That this latter is the case I am led to believe by the fact that in Mashonaland only the type form occurs, and there *esebria* is also absent; whereas along the south-east coast, where the latter is plentiful, *lycia* occurs, and when I met with it in Durban I was struck with its resemblance on the wing to the whiter specimens of *esebria*, though this is not so apparent in the cabinet.'

In describing the scents noticed in connexion with certain African butterflies, Dr. Dixey

says (Proc. Ent. Soc., 1906) that 'Dr. Longstaff found a slight snuffy scent in the male of *Acraea encedon* (Linn.), and an evanescent disagreeable odour, not very strong, in the female when crushed.' The yellow juice of this species is said by Marshall to be slightly bitter, but not very markedly so. During the visit of Drs. Dixey and Longstaff to South Africa in 1905, *A. encedon* was several times observed. At Durban two examples were taken, and they remarked that it was 'so successful in its mimicry of *L. chrysippus* as at first to make one of us believe it to be that species.' On another occasion a small female of *chrysippus* was mistaken for *encedon*. At Congella, three miles to the west of Durban, three examples were taken, and the authors remark that it 'is a feeble insect, with slow flight, but it again succeeded in passing itself off (momentarily) as *chrysippus*.'

The larva and pupa have been figured by Lieut.-Col. J. M. Fawcett (Trans. Zool. Soc., 1900), and are described as follows:—

'Larva. Slaty black with a yellow lateral line above prolegs and claspers. On each segment three deep black, fine transverse lines enclosing two white patches dorsally and two yellow patches laterally. On the centre black line of each segment are placed six black spines (branched). Head, thoracic legs, and claspers, black.

'Pupa. Waxy white, with the usual fine black lines on the wing covers, and black spots with orange centres on the abdominal segments.'

The larva feeds on a species of *Commelina*, a common weed in gardens at Maritzburg. This author describes the butterfly as one of the commonest in Durban. The insect has an exceedingly wide range, and may be said to be distributed over the greater part of Africa.

MIMACRAEA MARSHALLI.

Trimen, Trans. Ent. Soc., p. 13, pl. 1, f. 9 (1898).

Aurivillius, Rhop. Aeth., p. 266 (1898).

var. *dohertyi*.

Rothschild (species), Nov. Zool., viii, p. 215, pl. ix, f. 3 (1901).

Plate III, Figs. 6, 7.

The genus *Mimacraea* was founded by Butler in 1872, giving *M. darwinia* as the type. The genus belongs to the family *Lycaenidae*, and all the species so far known have a more or less Acraeine appearance, in many cases so perfect as to be extremely deceptive. *M. marshalli* is a very beautiful insect, bearing a strong resemblance when on the wing to a small specimen of *chrysippus* or to *A. encedon*. The species was discovered by Marshall in Mashonaland, and he gives the following interesting account of its capture in a letter to Professor Poulton in 1897: 'Whilst strolling along the narrow belt of thick bush which there fringes the river (Mazoe Valley), I saw flying leisurely in front of me what I took to be a very small and brightly coloured *Limnas chrysippus*. I coveted it, and a few seconds later it was in my net, through the folds of which I could but indistinctly see it, so that I was still deceived. But no sooner had my finger and thumb met across its thorax than my heart beat high with that keen excitement that every ardent entomologist feels when he has found some unexpected treasure, for I knew I had got a new mimic of *chrysippus*.'

Such an account is specially interesting as coming from one familiar with the habits of butterflies in their native haunts, and the fact that the collector was himself deceived by the appearance of this Lycaenid when on the wing, shows the value of its colouring as a protective disguise. *M. marshalli* presents some points which favour a closer resemblance, especially on the underside, to *Acraea encedon* than to *D. chrysippus*, though in the bright

golden colour of the wings it resembles the paler coloured form of the latter. It is described as essentially a woodland, but not a forest insect. When undisturbed it flies slowly like *D. chrysippus*, but when alarmed it flies with considerable speed and dodges with great dexterity, sometimes flying right over the tops of the trees. It has a habit of settling on the far side of a tree, making it difficult to follow, and owing to the fact that the upper wings are depressed within the lower ones, thus hiding the white patch, it becomes when at rest exceedingly inconspicuous. Marshall originally described it as settling on the tree trunk head downwards, but this is not invariably the case, as Mr. Neave on one of his African expeditions succeeded in photographing the insect at rest on a tree trunk. In this picture the butterfly is certainly in the ordinary position. *M. marshalli* remains a rare insect. Marshall took some fifteen examples, and about twenty specimens were secured by Mr. Neave in the Upper Congo. Perhaps about five other examples are known.

The form *dohertyi* figured on Plate III, Fig. 7, was first described by Rothschild, and was captured by Doherty in British East Africa. It is interesting as showing a development analogous to the *dorippus* variety of *D. chrysippus* and the *daira* form of *A. encedon*. The form is so rare that little appears to be known of its habits, though on general grounds the supposition that it has been developed under the influence of *daira* is irresistible. The formerly existing white sub-apical bar can be distinctly traced near the costa of the fore-wing.

In the cabinet and when viewed separately it might be supposed that *M. marshalli* and *A. encedon*, owing to their small size, would not present very good imitations of *D. chrysippus*. Mr. Neave, however, has shown me a very remarkable group captured in the Lualaba Valley on the Upper Congo. Amongst a large number of *D. chrysippus* there are also eight examples of *Mimacraea marshalli*, fourteen of *Pseudacraea poggei*, and five of *Acraea encedon*. The general effect of the group as seen together is that they are all alike, and when they are arranged in haphazard manner there is a distinct sense of effort in counting the respective numbers of the different species. I know no instance which could illustrate more forcibly the reality of the resemblance.

Another *Mimacraea* recently described by Druce and named *skoptoles* (Trans. Ent. Soc., 1907, p. 78) bears a strong superficial resemblance to *marshalli*, though it is differently marked on the underside.

ARGYNNIS HYPERBIUS.

Linnaeus, Cent. Ins., p. 25 (1763).

Linnaeus (*niphe*), Syst. Nat., ed. 12, p. 785 (1767).

Drury, Ill. Exot. Ins., i, p. 12, pl. 6, f. 1 (1773).

Linnaeus (*argyrius*), Iter. Chin., p. 10 (1768).

Drury (*argyrynnis*), Ill. Exot. Ins., i, p. 12, pl. 6, f. 2 (1773).

Godart (*tephnia*), Enc. Meth., ix, p. 262 (1819).

Moore (Metamorph.), Lep. Ceylon, i, pl. 31, f. 2 B (1881).

Aurivillius (Synonymy), Rhop. Aeth., p. 127 (1898).

Plate II, Fig. 13, ♀.

This butterfly abounds in the Oriental region, but in Africa it only occurs in Abyssinia. The figure on Plate II is from an Asiatic specimen, but I do not think the Abyssinian form varies greatly from this in appearance. As in many other cases, only the female exhibits mimetic tendencies, the male being without the black and white apex, and presenting the ordinary aspect which characterizes the genus *Argynnis*.

In describing the allied form *Argynnis inconstans*, which occurs in Australia, Butler

remarks that the female of that species resembles the male, and does not show any modification towards *D. chrysippus*; a fact which he explains by the non-occurrence of the model in that region. It is true that the typical form of the Danaïne is not found in that continent, but the form *D. petilia*, Stoll., does occur there. *D. petilia* seems to be more allied to the dark form *cratippus* which is found in Java, and the more reasonable supposition seems to be that either the extension of *petilia* to Australia is too recent to have affected the *Argynnis*, or that the latter is, as Butler described it, a distinct species; and since it has become established in Australia before the advent of the Danaïne, mimicry of the latter is unnecessary for its continuance. In Southern India there are females of *A. hyperbius* which resemble the males, as well as *chrysippus*-like forms, thus showing a more primitive condition than that obtaining in other portions of the range of the species. In Java, where *D. chrysippus* is represented by its peculiarly dark *cratippus* form, the female of *A. hyperbius* is much deeper and richer in colour. Speaking of the female of this species, De Nicéville remarks, 'there is no doubt that this distinctive type of coloration has been acquired by the female as a protection against its enemies, as, on the wing, that sex passes very well for a *Danaïs chrysippus*, which is a highly protected butterfly.'

In the Journ. Bombay Nat. Hist. Soc., 1890, Mr. J. Betham writes, 'The male has all the characteristics of the typical fritillary, dashing about in flight and fanning its wings when settled, just in the same sharp manner. The female is a more or less close imitation of *Danaïs genutia*,¹ and in flight looks very like the butterfly it mimics.' Commander J. J. Walker, writing in Trans. Ent. Soc., 1895, says, 'The female bears a striking resemblance to *Cethosia biblis*,² as well as to *Danaïs chrysippus* when on the wing.'

At the meeting of the Entomological Society in May, 1909, Mr. T. B. Fletcher exhibited females of *A. hyperbius* taken in Ceylon, and stated that under natural conditions the likeness between model and mimic was exceedingly close and deceptive, and that on his first acquaintance with the insect he was entirely deceived until it settled on a flower. He also remarked that the flight of the female is slow, and quite different from the sailing flight of the male. When viewed in the cabinet *A. hyperbius* is not a particularly good mimic of *D. chrysippus*, so that the above observations by those who have seen the species alive are the more interesting as indicating indirectly how efficient must be the more accurate imitation of such species as *H. misippus* and others already described.

ACRAEA MIMA.

Neave, Proc. Zool. Soc., pl. 1, ff. 8, 9 (1910).

Plate III, Fig. 5, ♂.

This beautiful and distinct species of *Acraea* was taken by Neave in North-East Rhodesia, and is described by him in his very extensive paper in Proc. Zool. Soc., 1910.³

The figure on Plate II shows the upperside of the male. On the underside the spots are more distinct. The fore-wing has the basal area pink, and the apical region sulphur yellow with ochreous internervular rays. The margin black. The hind-wing is pinkish-

¹ A species allied to *D. chrysippus* and somewhat resembling it.

² A species which itself mimics *D. chrysippus*. The family facies of the genus *Cethosia* are such as to render mimicry of *chrysippus* very easy, and in one

species, viz. *C. penthesilea*, the resemblance is remarkably accurate.

³ 'Zoological Collections from Northern Rhodesia and Adjacent Territories. Lepidoptera Rhopalocera.' S. A. Neave, Proc. Zool. Soc., 1910.

yellow, the margin bearing seven sulphur yellow spots surrounded with black. The base rose pink. In the female the upperside is brownish and lacks the beautiful rose tint of the male. The markings are similar, but more suffused and dusted with black. The white bar is larger, extending across the space between the second and third median. The underside is as in the male, but all the colours are duller. The body is black above and ringed and spotted with white. Pale ochreous below.

This butterfly is described as being very like *Mimacraea marshalli* when on the wing owing to its rosy tint. It forms an interesting addition to the mimetic group which surrounds *D. chrysippus*. At present it is extremely rare, only four males and three females having been taken.

ACRAEA WIGGINSI.

Neave, Novit. Zool., vol. xi, p. 326 (1904).

Neave, Trans. Ent. Soc., p. 215 (1906).

Plate III, Fig. 4.

Two females of this species were taken by Dr. Wiggins, one in the Tiriki Hills and one at Kisumu in 1903. Though the pattern of the wings is somewhat indefinite there can be no doubt that the insect is developing the characteristic features of the *chrysippus* group. The male which is in the Rothschild collection at Tring does not differ appreciably from the female in appearance.

COOKSONIA TRIMENI.

Druce, Trans. Ent. Soc., p. 256, pl. xiii, f. 3 (1905).

Plate III, Fig. 8.

The genus *Cooksonia* was founded by Druce in 1905 on the single female he then figured and described, which was taken in North-East Rhodesia in 1903, and I am indebted to that author's kindness for the opportunity of figuring the species in the present work. As will be seen, this insect bears the same *chrysippus*-like appearance which is exhibited by *Mimacraea marshalli*, though the underside has a distinctly Acraeine appearance. The white bar does not appear on that surface, but is replaced by a dusky apical area, and the hind-wing is bordered by three sinuous lines of black, and bears in the basal area several black spots of a distinctly Acraeine pattern. If the insect, as seems probable, habitually settles with the fore-wings dropped within the secondaries, the resemblance to an *Acraea* must be very perfect. The species adds another and very remarkable instance to the many known cases of Lycaenid mimicry in the African region.

DIESTOGYNA IRIS.

Aurivillius, Arkiv Zool., i, 1903.

Plate II, Figs. 14, 15.

Whilst many species of this genus, especially in the females, exhibit a tendency to a *chrysippus*-like pattern, this species has developed the typical golden colour and the black and white apical bar to an extent which brings it decidedly within the *chrysippus* association, and Mr. Neave, who took a long series of both sexes, tells me that the female is very like its model when on the wing. He also states that it does not occur in forest, like most of its allies, but usually settles on the ground with expanded wings showing its

chrysippus-like coloration. As will be seen from the figures, the contrast between the sexes is very great, and reminds us of the marked difference between the male and female *misippus*. *D. iris* appears to be a somewhat local insect, though not rare in its regular habitat. Other members of this genus exhibiting a somewhat *chrysippus*-like pattern are *D. veronica*, *D. tadema*, and *D. karschi*, some of the females of these species closely resembling that of *D. iris*. The latter species was taken by Mr. Neave at Lake Bangweolo in North-East Rhodesia, whilst the other species named are West African forms.

The females of some species of *Euryphene*, notably *E. senegalensis*, Schaeffer, and *E. chriemhilda*, Staudinger, occurring near Mombasa, have a somewhat *chrysippus*-like pattern, though their flight and habits are such as to somewhat discount the value of their appearance in this respect. They fly rapidly close to the ground in woodland or forest country, As Rogers has, however, pointed out (Trans. Ent. Soc., p. 521, 1908), it is difficult to account for the female pattern unless the insects do gain some advantage through their likeness to the Danaine model.

Other forms showing an approximation towards the *chrysippus* pattern are certain forms of the female of *Acraea esebria*, which have a white sub-apical bar in the fore-wings, also the female of *Acraea petraea*, which bears a close resemblance to *A. encedon*. The opponents of mimicry have sometimes asked for proof that supposed mimetic forms are found together in nature. Ample proof of this elementary fact is furnished by the large collection of groups of mimetic butterflies taken on the same day and now preserved in the Hope Museum at Oxford. It is, however, especially interesting to note that these groups include associations taken by Mr. Marshall at Malvern, Natal, one of which contains *D. chrysippus*, *H. misippus*, *A. esebria*, and *A. encedon*, whilst another includes the above-named species and also *Acraea petraea*, showing very clearly the incipient mimicry of the latter species and the female *A. esebria*.

THE ALETIS GROUP.

ALETIS HELCITA.

Clerck, Icon. Ins., ii, pl. 39, f. A (1759).

Plate III, Fig. 11.

This day-flying Geometrid moth forms the centre of an interesting mimetic association.¹

Forms of *Aletis* appear to be common throughout Tropical Africa, and the genus is characterized by brilliancy of colour, relative abundance, and carelessness of pursuit, from which it may be concluded that the species enjoy considerable freedom from attack. Many of them are imitated also by other moths, notably *Phaegorista similis* (= *helcitoides*) and *Xanthospilopteryx poggei* (= *Eusemia falkensteinii*).

¹ Instances of mimicry between moths and butterflies are by no means uncommon, and in the Asiatic and Neotropical regions present some very remarkable examples of the phenomenon. The sub-family *Pericopinae* in South America includes many species which in colour and markings resemble certain Heliconid butterflies with the most perfect accuracy. Perhaps the most wonderful instance of mimicry between a butterfly and a moth is that furnished by *Alcidis aurora* and *Papilio laglaizei*,

both of which insects occur at Milne Bay, New Guinea. The resemblance on both surfaces is very perfect; but the most remarkable feature is the fact that the underside of the body of the moth is bright orange colour, whilst that of the butterfly is pale green, but the latter has a bright orange patch on the inner-margin of the hind-wings which exactly fits against the abdomen when the insect is at rest, thus causing it to appear to have an orange-coloured body like the moth.

EUPHAEDRA RUSPINA.

Hewitson, Exot. Butt. (*Romalaecosoma*), pl. 11, ff. 6, 7 (1865).

Staudinger, Exot. Schmet., i, p. 148, pl. 51 (1885).

Aurivillius, Rhop. Aeth., p. 185 (1898).

Plate III, Fig. 12.

The genus *Euphaedra* comprises a number of large-bodied butterflies essentially natives of Tropical Africa, about forty species being described. They are for the most part dark coloured with a greenish or bluish gloss, and with a pale sub-apical bar on the fore-wings. Some species have more or less red on the wings and the body conspicuously spotted with white. Amongst the latter we find *ruspina*, which presents in both sexes and on both surfaces a remarkably close resemblance to the moth *Aletis helcita*. The species was described and figured by Hewitson in 1865. The mimetic tendency of the genus appears to have reached its maximum development in the present species. In the closely allied *E. eleus*, Drury, the female is very similar to *ruspina*, but the male still retains the typical greenish suffusion on the apical area of the fore-wings. In both the male and female *eleus* the sub-apical white bar is less conspicuous, and the mimicry of *Aletis* does not extend to the under surface as in *ruspina*. In a third species, *E. zampa*, Westw., the transition is still more beautifully illustrated. In this species the female has the red ground-colour with a narrow white sub-apical bar on the fore-wings. In the male the typical dark-green colour prevails, the red being only present as a basal suffusion on the hind-wings and an exceedingly faint but similar suffusion on the fore-wings. The sub-apical bar is formed by four small separate spots of a creamy white colour. In these three species there is, therefore, a perfect gradation from the typical green of the genus to the brick-red which in *ruspina* produces in both sexes such a striking resemblance to the moth *A. helcita*, whilst in each case, as we should expect, the female shows the most advanced mimetic development. As is usual in genera exhibiting mimetic tendencies, the species of *Euphaedra* are exceedingly liable to variation, showing thereby the comparative instability of pattern which enables the selective forces to produce such striking counterfeits of other and better protected species. *Ruspina* is a West African insect, the example figured was received from the Gaboon district.

TELIPNA SANGUINEA.

Plötz, Stet. Ent. Zeit., xli, p. 198 (1880).

Smith and Kirby, Rhop. Exot., i, p. 2, pl. 1, ff. 3, 4 (1887).

Dewitz (*anneckeri*), D. E. Z., xxx, p. 427, pl. 11, ff. 2, 2 a (1886).

Staudinger (*acraea*), Exot. Schmet., i, pl. 94 (1887).

Aurivillius, Rhop. Aeth., p. 257 (1898).

Plate III, Fig. 13.

The African region is remarkable for the prevalence of Lycaenid mimics, a fact which has been discussed at some length by Professor Poulton (Trans. Ent. Soc., 1902). Having shown that the fact is not due to unusual richness of species, he arrives at the conclusion that it is caused in all probability by the 'number of feasible models of moderate and small size furnished by the abundant *Acraeinae* of Africa'. He also points out that the habits of the latter assist the growth of mimetic forms. 'The numerous low-flying and low-settling *Acraeas*, resting at night on grass stems, have precisely the mode of life which is well known to be characteristic of such a large number of *Lycaenidae*.'

T. sanguinea would appear to be a rather variable species, or there may be several closely allied forms. Haase depicts it as having a bright red ground-colour whilst the figure in Kirby and Smith's 'Rhopalocera Exotica' shows the species of a dark brick-red. Those authors

describe a variety of this insect (*bimacula*, Plötz), in which the ground-colour of the upper-side is vermilion, and also certain examples of this or a closely allied form which is half as large again as the specimens figured in their work, at the same time expressing the opinion that this form is identical with the *bimacula* of Plötz above mentioned. Such a species would undoubtedly bear a still closer resemblance to *A. helcita*. The specimen figured is a West African example in my own collection.

The sexes do not greatly differ in appearance.

There are several African *Lycaenidae* having this type of colouring, which has probably in the first instance arisen as a development in the direction of a general Acraeine appearance, and then produced as in the present case the mimicry of *A. helcita*. The lately described *Telipna nyanza*, Neave, is somewhat similarly coloured, though paler, and so more like the yellow forms of *Aletis*. It was taken at Entebbe.

PSEUDALETIS AGRIPPINA.

H. H. Druce, Ent. Mo. Mag., p. 259 (1888).

Staudinger (*tricolor*), Iris, iv, p. 143, pl. 1, f. 5 (1891).

Aurivillius, Rhop. Aeth., p. 311 (1898).

Plate III, Fig. 14, ♀.

The very remarkable Lycaenid genus *Pseudaletis* was founded by Druce on this species. In all the other species (except *nigra*, Holl., which is principally black) the ground-colour is white or yellowish, but *P. agrippina* has developed a brick-red ground-colour which, combined with the white-spotted black border, produces a very close resemblance to *Aletis helcita*, as pointed out by the author in his original description. The two short black tails, conspicuous enough in the cabinet, are probably invisible when the insect is flying or settled with open wings. The species is found in Cameroon, and *helcita* is abundant in the same region. *P. agrippina* is an exceedingly rare insect. My figure is from an example in the British Museum, in which collection there are two specimens. The male was described by the late Dr. Staudinger under the name *tricolor*.

EUPTERA CROWLEYI.

Kirby (*Cymothoe*), An. N. H. (6), iii, p. 247 (1889).

Smith and Kirby, Rhop. Exot. (*Cymothoe*), p. 2, pl. 1, f. 5 (1890).

Aurivillius, Rhop. Aeth., p. 216 (1898).

Plate III, Fig. 15.

This extremely rare butterfly was taken at Agowe in Dahomey and the male is not certainly known. Dr. Jordan has shown me a male *Euptera* of which he thinks *E. crowleyi* is probably the female. In the absence of more extensive material it is not easy to determine whether this species is influenced most by *D. chrysippus* or by a species of *Aletis*, in which the ground-colour is yellow rather than red as in *helcita*. I have figured the butterfly in order to draw attention to an exceedingly rare species in the hope that further information may soon be obtained with regard to the development of a pattern which I am convinced is mimetic in character.

MIMICRY IN OTHER SPECIES OF EUPHAEDRA.

EUPHAEDRA EUSEMOIDES.

Smith and Kirby, Rhop. Exot., viii (*Euryphene*), p. 1, pl. 1, ff. 1, 2 (1889).
 Aurivillius, Rhop. Aeth., p. 185 (1898).

Plate III, Fig. 10.

I received this butterfly from Sierra Leone in the same small collection which contained the moth *Phaegorista agaristoides*, Boisd., which I have illustrated at Fig. 9. The general resemblance between the two insects, though not so remarkable as that between *E. ruspina* and *A. helcita*, is quite sufficient to be noteworthy when it is borne in mind that several species of *Euphaedra* more or less approach in pattern these day-flying moths. The Eastern form of *Euphaedra zaddachi*, named *crawshayi* by Butler, bears a strong resemblance to species of the day-flying moths of the genus *Xanthospiloptyx*. Writing in 1908 to Professor Poulton, Mr. Neave, who was then collecting in North-East Rhodesia, gives some very interesting particulars with regard to a *Euphaedra*, probably allied to *E. eusemoides*, which he had observed in that region. He says,¹ 'The interesting thing about the above species of *Euphaedra* is that it differs in its *habits* from its allies. It spends little or none of its time on the ground as they nearly all do, but is constantly flying round trees and large shrubs—the *very thing its model is fond of doing*. One or two of my specimens were caught by sending small boys up trees after them.' Such testimony is exceedingly valuable, since it has been stated that although some butterflies do resemble moths, the difference in their habits and flight is such as to discount any theory as to the mimetic nature of the resemblance.

THE A. ALCIOPE ASSOCIATION.

ACRAEA ALCIOPE.

Hewitson, Exot. Butt. *Acraea*, pl. 1, f. 4, 5 (1852).
 Ward (*cydonia*), Ent. Mo. Mag., x, p. 59 (1873).
 Butler (*macarina*), Proc. Zool. Soc., p. 221,
 pl. 17, f. 6 (1868).
 Aurivillius (*alciope* var.), Ent. Tidskr., xiv,
 p. 278, f. 6 (1893).
 —Metamorph., l. c., p. 279, pl. 5, f. 3, 3a, 3b
 (1893).

Aurivillius, Rhop. Aeth., p. 116 (1898).
 Staudinger (*aurivillii*), Iris., ix, p. 209, pl. 2,
 f. 2 (1896).
 Aurivillius, Rhop. Aeth., p. 117 (1898).
 Smith and Kirby (*Planema alicia*), Rhop. Exot.,
 p. 30, *Acraea*, pl. 8, ff. 9, 10, 11 (1901).
 Roth. and Jord. (subsp. *schecana*), Nov. Zool.,
 p. 184 (1905).

Plate III, Figs. 16, 23. Plate VIII, Fig. 4.

The mimetic relations of *Acraea alciope* are exceedingly complicated. In West Africa the male is apparently the model for the female of *M. fulvaria*, whilst the male of the latter mimics a *Planema*. The West African female of *A. alciope* figured on Plate III, Fig. 23, also mimics a *Planema*.² This form is very variable, and it would be perhaps more correct to say that it presents a Planemoid pattern rather than to assume that it definitely resembles a particular model. Most of the examples which I have examined in the National Collection are very like the *Planema excisa* of Butler. When inspecting considerable numbers of *A. alciope* for the purpose of the present account, I was struck by the fact that the males were common, and not greatly varying from as far west as Ashanti, right across to Uganda,

¹ Proc. Ent. Soc., p. lxxx, 1908.

² Probably a form of *Planema salvini*, Butl., figured on Plate III, Fig. 19. The specimen is from Sierra Leone. See *Planema alcinoe*, p. 78.

but that all the females were from the west coast only, and none of the Uganda specimens had females definitely assigned to them. The *Acraea* from Uganda which was represented by females only, and which could be associated with *A. alciope*, was *A. aurivillii*. I therefore consulted with Dr. Jordan on the subject, and he very kindly assisted me to make an examination of the very large amount of material in the Tring Museum, where I found that he had already placed *alciope* and *aurivillii* together as closely associated. An examination of the types of *Planema alicia*, Smith and Kirby, also showed that the alleged male of that species was in fact a female. The material in the National Collection was then examined, and the same species were there found to be closely associated. The result of the whole investigation was therefore that *A. aurivillii*, Staud., is the eastern female of *A. alciope*. The *Planema alicia* of Smith and Kirby cannot stand, since it is not a *Planema* but an *Acraea*; there is already an *Acraea alicia*, Sharpe, the alleged male is a female, and the specimen described as a female is not separable from *A. aurivillii*. The supposed male *A. alicia* is a female variety which occasionally occurs at Entebbe. We thus have the very remarkable result that the female *A. alciope* in the West has become modified in mimetic association with a *Planema* which is probably a form of *P. salvini*, whilst in the East the *aurivillii* form is developed in mimicry of *Planema poggei*. With regard to the western female, specimens from Fernando Po seem to show nearly every gradation from the western type to something very near *A. aurivillii*, which latter was originally described from inner Cameroon. Amongst the forms examined the following varieties may be specially mentioned.

1. The ochreous colour of the male extends nearly all over the hind-wings, leaving only the dark internervular rays and a faint dusting of black scales on the margin. The fore-wing hind-marginal black becomes dentated into the ochreous colour, and the dark basal area is much broken up and suffused.

2. The fore-wing band is almost as in *aurivillii*, and the hind-wing margin is beginning to be more pronounced.

3. The fore-wing band is almost white. The hind-wing band is also white, and all the other pale markings whitish.

4. The fore-wing band is still much broken up, especially by a row of irregular black spots in the middle of the wing. (These spots survive in *aurivillii* on the underside as dark markings on the basal side of the yellow bar). In this specimen the hind-wing remains white, and the example is almost perfectly intermediate between the Planemoid West African female and the *aurivillii* form. All the above four examples were taken at Fernando Po.

5. A specimen from Ashanti in which the fore-wings are like those of Fig. 23, Plate III, but the hind-wings are whitish. This is probably an aberration. All the other Gold Coast specimens are more like Fig. 23, and reddish rather than ochreous.

The subspecies *schecana* described from a male by Rothschild and Jordan is an Abyssinian form, somewhat paler than the western male, and with a wider black border in the hind-wing.

With the kind assistance of Dr. Jordan I have drawn up the following table of the forms of *Acraea alciope* :—

ACRAEA ALCIOPE.

alciope alciope. Ashanti to Upper Congo. ♀ always tawny. Band of fore-wing often obsolescent. At Fernando Po ♀ very unstable and presenting numerous varieties (= *cydonia*, Ward, = *macarina*, Butler).

alciope aurivillii. Inner Cameroon to Uganda. ♀ = *aurivillii*, Staud., white band on hind-wings. Has a female variety with tawny hind-wings.

alciope schecana. R. & J., Abyssinia. (Descr. from one ♂).

The larva and pupa are thus described by Professor Aurivillius : (l. c.)

'The larva is pale (yellowish?) with narrow dark transverse lateral streaks. The head, legs, and spines are black. The lower lateral spines, however, are only black at the ends. The spines are decidedly longer than the body diameter, and arise from brownish tubercles. The pupa has the usual black markings of *Acraeinae* pupae. The spots of the abdomen have pale centres, and the two dorsal rows converge forward, and there join in a black spot on the first segment. In the pale centres of the dorsal spots of segments 2-5 (6) are small pointed tubercles, which are largest at 2, and become gradually smaller posteriorly.'

MIMACRAEA FULVARIA.

Aurivillius, Ent. Nachr., xxi, p. 381 (1895).

— Rhop. Aeth., p. 266, pl. 6, f. 6 (1898).

Plate III, Fig. 18, ♂ (?), Fig. 20, ♀.

This very distinct *Mimacraea* is figured by Professor Aurivillius in his work on the African Butterflies, and as I was unable to obtain an example from which to make a drawing, he very kindly allowed me to make a copy of the figure in his work. Fig. 18 is drawn from an example in the Hope Department at Oxford. At first sight I took the latter form to be a distinct species, but on reference to the National Collection I found a similar specimen referred to the present species. Very little is known of this aberrant *Lycaenid*. There can be little doubt that the female mimics the male *Acraea alciope*, the female of which is itself involved in complicated mimetic associations with forms of *Planema*. Whether the insect shown at Fig. 18 is actually the male of *M. fulvaria* or not, the wonderful development of the Planemoid pattern on the underside is a most convincing instance of *Lycaenid* mimicry. I have illustrated at Fig. 17 a male example of *Planema macaria*, Fabr., from Sierra Leone, whence also the *Mimacraea* was received, in order to show the resemblance of the underside patterns. On the upperside the coloration may be said to be of a generally Planemoid appearance, and is somewhat intermediate between that of Fig. 19 and Fig. 17. The female *M. fulvaria* was received from Ubangi River in the Congo State, and is in a private Continental collection.

A. SOTIKENSIS AND M. POULTONI.

ACRAEA SOTIKENSIS.

E. M. Sharpe, Proc. Zool. Soc., 1891, p. 634,
pl. 48, f. 1 (1892).

Oberthür, Étud. d'Ent., xvii, p. 23 (1893).
Aurivillius, Rhop. Aeth., p. 105 (1898).

Plate III, Fig. 21.

This common *Acraea* occurs in large numbers in British East Africa. Mr. Neave has also taken it in North-East Rhodesia and in the upper reaches of the Congo. The males and females do not greatly differ in appearance, but in examining a long series the amount of red suffusion in the cell of the fore-wing is found to vary somewhat, as does also the depth of tone of the red colour. In one or two specimens there is also a distinct row of pale hind-marginal internervular spots in the hind-wing. In one example I have seen the discal band in the hind-wing is pale yellow, like the fore-wing sub-apical bar, being only slightly dusted with reddish towards the costa. This variety is of some interest, since it is apparently copied by a corresponding variety of *Mimacraea poultoni*. In the figure on Plate III the basal patch of the hind-wing and the inner-marginal patch of the fore-wing are scarcely as dark as in the majority of specimens, and the sub-apical bar of the fore-wing is of a somewhat brighter yellow.

MIMACRAEA POULTONI.

Neave, Novit. Zool., xi, p. 337, pl. 1, f. 18 (1904).

— Trans. Ent. Soc., p. 219 (1906).

Plate III, Fig. 22.

I have examined five examples of this interesting Lycaenid, and, judging by even so small a series, it appears to be a rather variable insect. Two of the specimens are like the figure, on Plate III, though one, a female, has the sub-apical bar a little deeper in colour. The species presents a beautiful mimetic resemblance to the model *A. sotikensis*, with which insect the original examples were taken at Nyangori. A third example, a female, has the inner-marginal patch of a paler orange, whilst the discal band in the hind-wings is the same colour as the sub-apical bar in the fore-wing, though suffused round the edges and along the nervules with a deeper orange tint. A fourth specimen, only lately received from Entebbe, has the ground-colour and the orange of the fore-wings darker and richer, and the sub-apical bar is also orange, whilst the discal band in the hind-wing is pale yellow, suffused with orange only close to the costa. Finally, a specimen in my own collection, from the same neighbourhood, has all the light markings of a pale yellow colour, only the inner-marginal patch in the fore-wings and the costal portion of the hind-wing being very slightly deeper in tint than the remainder. In all these examples the underside shows little or no variation. It will be seen that the third specimen resembles the variety of *sotikensis* already mentioned. The example with all the markings pale yellow is with difficulty distinguished from *Acraea viviana*, Staud., whilst if it be remembered that these butterflies come to rest with the fore-wings dropped back within the secondaries, thus showing only the underside of the latter, then the resemblance to *A. viviana* must be better even than that to *A. sotikensis*. *A. viviana* is found at Entebbe, whence I received the pale form of the Lycaenid. I have also seen an example of *M. poultoni* in the Tring Museum, which was taken in Cameroon, showing that the insect has a very wide range. This western specimen has the markings nearly all pale yellow, and it is difficult to distinguish it by its pattern alone from *A. viviana*, var. *karschi*, Auriv., which is found in the same district.

THE FORMS OF ACRAEA LYCOA AND ACRAEA JOHNSTONI.**ACRAEA JOHNSTONI.**

TYPE. *johnstoni johnstoni*. Godm., Proc. Zool. Soc., p. 537 (1885).

= *Planema telekiana*. Rogenhofer, Ann. D. K. K. Naturhist. Hofmus. Wien, p. 459, pl. 15, f. 4 (1891).

= *Acraea proteina* f. *semifulvescens*. Oberthür, Étud. d'Ent., xvii, p. 26, pl. 2, f. 21 (1893).

johnstoni, var. *confusa*. Rogenhofer, l. c., p. 459, pl. 15, f. 5 (1891).

= *johnstoni* ♀. Butler, Proc. Zool. Soc., p. 91 (1888).

= *proteina*. Oberth., Étud. d'Ent., xvii, p. 25, pl. 2, f. 14 (1893).

= *proteina* f. *flavescens*. Oberth., l. c., p. 26, pl. 1, f. 4 (1893).

= *proteina* f. *semialbescens*. Oberth., l. c., pl. 3, f. 29 (1893).

johnstoni, var. *fulvescens* = *proteina* f. *fulvescens*. Oberth., l. c., p. 26, pl. 2, f. 21 (1893).

johnstoni, var. *toruna*. Grose-Smith, Rhop. Exot., pt. lvii, *Acraea*, pl. 8, f. 1 (1901).

= *lycoa*, ♀ var. Butler, Proc. Zool. Soc., p. 731 (1895) = *lycoa* ab. *butleri*. Auriv., Rhop. Aeth., p. 115 (1898).

ACRAEA LYCOA.

TYPE. *lycoa lycoa*. Godt., Enc. Meth., ix, p. 239 (1819).

lycoa, var. *fallax*. Rogenhofer (*Planema*), Ann. D. K. K. Naturhist. Hofmus. Wien, vi, p. 459, pl. 15, f. 6 (1891).

= *kilimandjara*. Oberthür, Étud. d'Ent., xvii, p. 26, pl. 2, f. 17 (1893).

lycoa aequalis, Roth. and Jord.

R. and J., Novit. Zool., xii, p. 184 (1905).

Plate III, Fig. 24, 25, 26, 28. Plate VIII, Fig. 13.

In the 'Transactions of the Entomological Society', 1906, an exhaustive paper was published by Professor Poulton, on the forms of *P. dardanus* and *Acraea johnstoni*. There all the forms of *lycoa*, *johnstoni*, and *fallax* were fully dealt with, careful comparison being made of all the modifications geographically considered. The main conclusion was that they must all be regarded as specifically identical with the western *lycoa*. This species I have not figured, but it may be described as follows :—

The male is about the size of Fig. 23, Plate III. The ground-colour is pale umber-brown, somewhat redder in the hind-wings, and all the wings are more or less translucent. In the fore-wings there is a sub-apical bar of a much paler colour, separated into four spots by the intervening nervules, the first spot being a mere line between the first and second subcostals, the second, third, and fourth, much larger, and occupying the whole internervular space, and the fourth somewhat ovate, more distally placed than the rest, and nearly reaching the hind-margin. Between the first and second median a large pale mark well defined basally, but suffused towards the hind-margin. Beneath the first median another rather smaller mark, more distally placed, and nearly reaching the hind-margin. The hind-wing pale discally, and slightly suffused with brown towards the margin. Nervules and rays strongly marked. Several small black spots at the base and a black line in the cell. Body black above, orange beneath, and ringed and spotted with orange. In some examples the male is so nearly transparent as to have almost lost the pale spots in the fore-wing. The female is slightly larger and much blacker. The spots on the fore-wing are white, and there is a distinct white suffusion beneath the base of the second subcostal, making the sub-apical bar more continuous. The hind-wings are white with a broad blackish border extending to midway between the hind-margin and the end of the cell. About the anal angle and the inner-margin there is a slight reddish-brown suffusion, representing the reddish-brown colour in the male hind-wing. The base is powdered with brownish black, and bears a few small black spots.

The larva and pupa of *Acraea lycoa* are thus described by Professor Aurivillius¹ :—

'Larva. Yellowish without markings, head and spines black. The spines are scarcely as long as the diameter of the body.'

'Pupa with usual black markings; the black spots of the abdomen have pale centres and are irregularly angular; the abdominal segments 2-4 are armed with two short black spines yellow at the base.'

I propose to deal with *Acraea lycoa* and *Acraea johnstoni* together, as the similarity between the *fallax* form of *lycoa* and the *confusa* form of *johnstoni* have led to some confusion in nomenclature, and the present description of the forms will serve to explain some of the features whereby the two species may be distinguished. As already stated, Professor Poulton was led to believe, from an examination of the outward characteristics, that *lycoa* and *johnstoni* gradually merged one into the other, and were in fact conspecific. It was at his suggestion that I undertook a microscopical examination of the more minute structure of the insects in question, with the result that *lycoa*, with its forms *fallax* and *aequalis*, were found to be geographical races of one species, whilst *johnstoni* and its varieties, including the *Acraea toruna* of Grose-Smith, were found to be also conspecific though distinct from *lycoa*. Our present concern being with mimetic associations, I do not propose here to enter into the details of this systematic inquiry,² but must confine myself to a brief account of the peculiar modifications which the patterns of these butterflies undergo. The mimetic relations of these varieties have already been described by Professor Poulton (l. c.). In West Africa

¹ Ent. Tidskr., xiv, p. 278, pl. 5, ff. 2, 2a, 2b (1893).

² A paper dealing with the subject at some length is in course of preparation.

the female *A. lycoa* is probably synaposematic with the black and white forms of *Amauris* and *Planema*, but as we pass eastwards the pattern gradually changes in both sexes, though less rapidly in the male. The spots and hind-wing patch become less indefinite in outline, and much more clearly separated, whilst the latter marking undergoes a change from white to yellow, and the ground-colour becomes much darker. From Sierra Leone down to the French Congo and across the Congo State comparatively little change is observable, but at Entebbe there is sufficient modification to enable the examples from that locality to be distinguished from the extreme western forms. At Kilimanjaro we have a further development to the *fallax* form of Rogenhofer, figured in Plate III. In this the spots are clearly defined in both sexes, but they remain white in the female and pale yellow in the male. The hind-wing patch in both sexes is pale yellow. The insect has become modified so as to resemble the dominant eastern Danaines, *Amauris echeria* and *A. albimaculata*. Up to this point the species is sexually dimorphic, but in the remarkable Abyssinian subspecies, *A. lycoa aequalis*, R. and J., this character disappears, and we have both sexes alike in coloration. The ground-colour is brownish-black, the hind-margin of the secondaries having, especially in the female, a tendency to a reddish-brown colour. The spots and hind-wing patch are clearly defined, and of a rather deeper yellow than in the other forms.¹

In the case of *A. johnstoni* there is no sign of sexual dimorphism. All the varieties occur in both sexes, nor is there good reason to separate them into geographical subspecies, with the exception of the *toruna* form. This latter occurs at Toro in Western Uganda and also in the Urundi country between Lake Kivu and Lake Victoria Nyanza, to the north-east of Lake Tanganyika. As the figure on Plate III shows, it is a very perfect mimic of *Planema latifasciata*, Sharpe (also figured on the same plate), which occurs in the same region. In the Tiriki Hills and on Kilimanjaro the commonest form is the *confusa* of Rogenhofer, a white- or yellow-spotted form very closely resembling *lycoa fallax*, and mimicking the same Danaine species. Here we find also the typical *johnstoni* of Godman (= *semifulvescens*, Oberth.), some examples of which, having the hind-wing discal area white, instead of yellowish as in the type, show a modification in the direction of *Planema poggei*. This form is illustrated on Plate VIII, Fig. 13. The form *fulvescens*, Oberth., Plate III, Fig. 26, has almost lost the spots of the fore-wing and the patch in the secondaries, and is synaposematic with *Danaida chrysippus* f. *dorippus* and *Acraea encedon* f. *daira*. All the *johnstoni* forms, except some examples of *toruna*, have the distal outline of the hind-wing patch somewhat edentate, giving it a quadrate appearance.

There is in the Tring Museum a family of *Acraea johnstoni* bred from a batch of ova at Nguelo, Usambara. It consist of nine individuals, comprising two ♂♂ and one ♀ *fulvescens* of fairly typical form, one ♀ *fulvescens* somewhat intermediate to the type, two ♂♂ and one ♀ resembling the type form (= *semifulvescens*), but with the discal patch of the hind-wings whiter, one ♂ of the *confusa* form, spots and hind-wing patch yellow, and one ♀ of the *confusa* form with all the markings white. The causes underlying the development of these polymorphic forms remain somewhat obscure. We can only at present call attention to the fact that of the innumerable patterns which might conceivably be assumed, only those are developed which resemble the appearances of dominant protected forms, and we must await the time when further investigation based on extensive breeding experiments may throw additional light on these complicated associations.

¹ It is interesting to note that the *steckeri* form of *A. echeria* occurring in Abyssinia is characterized by having the markings of a deeper and duller ochreous than in other forms of the same species, whilst it is

entirely devoid of white spots. It is doubtless in mimicry of this form that the white spots have disappeared from the female *lycoa aequalis*.

ELYMNIAS PHEGEA.

Fabricius, Ent. Syst. 3, Part I, p. 132
(1793).

Donovan, Ins. Ind., pl. 31, f. 1 (1800).

Mabille, Hist. Mad. Lep., i, p. 80 (1887).

Aurivillius, Rhop. Aeth., p. 45 (1898).

— (var. *intermedia*), l. c.

Westwood (*bammakoo*), Gen. D. Lep., p. 405,
pl. 68, f. 3 (1851).

Plate III, Fig. 29. Plate VIII, Fig. 10. Plate VII, Fig. 9.

I can find no very satisfactory reason for separating the forms of this butterfly into two species, as has been suggested, by distinguishing *phegea* from *bammakoo*. There are certainly three marked varieties, but an examination of a large series discloses numerous intermediate forms. Fabricius's description includes black and white and black and ochreous forms, whilst Hewitson's figure is of the ordinary Sierra Leone form, usually black and white, of which I have received considerable numbers from that region. Staudinger's variety, which he calls *phegea*, and to which Professor Aurivillius gives the name *intermedia*, has the ground-colour of the hind-wing, and the inner-marginal patch of the fore-wing ochreous, whilst the sub-apical bar is white, and to this extent the form exhibits an approach to *D. chrysippus*. The genus *Elymnias* is essentially Oriental, and its species provide some of the most curious examples of mimicry in that region. It would not be too much to say that the entire genus lives by deception, practically every species being modified in the direction of some dominant model. The three most marked and constant varieties of *E. phegea* in Africa appear to be—

1. The black and white form, Plate VII, Fig. 9. This form occurs throughout the range of the species. In the west, as, for instance, at Sierra Leone, it is a member of the group in which we find *Planema epaea* ♀, *Papilio cynorta* ♀, and some other black and white *Planema* forms. The same variety occurs at Entebbe, where it is a close mimic of the eastern form of *Planema alcinoe*.

2. A variety in which the white marks are replaced by ochreous. This form may be said to have two sub-varieties, one of which (Plate III, Fig. 29) has the sub-apical bar and the inner-marginal patch confluent, and forming a continuous discal band. This arrangement provides a very good resemblance to *Acraea alciope* on the one hand, and on the other, when the ochreous colour is somewhat richer, as it frequently is, to the general appearance of many of the large male *Planemas*. The second sub-variety has the sub-apical and inner-marginal patches distinctly separated, and of a richer colour, giving it a very marked resemblance to the widely distributed *Planema tellus*.

3. The third variety, occurring at Entebbe, is perhaps the most interesting, and is shown at Plate VIII, Fig. 10. Here the white of the fore-wings has become the beautiful orange ochre of *Planema poggei*, a modification which we should certainly expect to occur in the event of so adaptative a species as *phegea* coming in contact with that model.

It is a curious fact that in spite of the apparent adaptability of the species of *Elymnias* to the general colour patterns of dominant forms, they almost always retain their characteristic shape, and their mimicry is always of a nature which may be described as a sketch of the model. Many of the Oriental species, whilst unmistakably mimicking species of *Danais* and *Euploea*, have all the markings suffused in outline, and this, combined with the serrated margin of the wings, gives them the appearance of tattered and worn examples of their respective models. It would be interesting to discover whether a tattered appearance is in itself any protection, as suggesting to enemies an insect which has been tried by others and found unpleasant. The sexes of *E. phegea* do not differ in pattern.

*THE M. FORMOSA GROUP.***MELINDA FORMOSA.¹**

Godman, Proc. Zool. Soc., p. 183, pl. 19, f. 1 (1880).

Aurivillius, Rhop. Aeth., p. 33 (1898).

Neave, Trans. Ent. Soc., p. 215, pl. x, ff. 1, 1a (1906).

Plate IV, Figs. 1, 2.

MELINDA MERCEDONIA.

Karsch, Ent. Nachr., xx, p. 225 (1894).

Aurivillius, Rhop. Aeth., p. 33, f. 3 (1898).

Neave, Trans. Ent. Soc., p. 215, pl. xii, f. 4 (1906).

Plate IV, Fig. 3.

These two Danaine butterflies are very distinct in appearance from any of the other members of their race in the African region. Neave has expressed the opinion that they are probably modifications from *Tirumala petiverana*, that being the ancestral form, though Marshall has pointed out (Trans. Ent. Soc., 1908, p. 125), that though *T. petiverana* has so wide a distribution in Africa it has not produced any really close mimics, certainly none that can be compared with *P. rex* and *P. mimeticus*, which are such accurate mimics of *M. formosa* and *M. mercedonia*. The two latter butterflies were at one time considered great rarities, but though extremely local they are now known, in the case of *M. mercedonia* at least, to be very plentiful in their respective localities. As will be seen from the figures, the female *M. formosa* differs from the male in the more rounded appearance of the wings and somewhat larger extent of the basal dark ochreous colour in the fore-wings. *M. mercedonia* is now received in considerable numbers from the neighbourhood of the north-west shore of Lake Victoria Nyanza. In a large collection I received from Entebbe the species was exceedingly common. The female is so far much rarer than the male, though it has lately been taken more frequently. It differs only very slightly, and principally in the rather paler ground-colour of the hind-wings.

PAPILIO REX.

Oberthür, An. E. Fr. (6) vi. Bull., p. 115 (1886).

— Étud. d'Ent., xii, p. 2, pl. 1, f. 2 (1888).

Aurivillius, Rhop. Aeth., p. 461 (1898).

Plate IV, Fig. 5, 6.

PAPILIO MIMETICUS.

Rothschild, Entomologist, xxx, p. 165 (1897).

Novit. Zool., iv, p. 315, pl. 4, f. 2 (1897).

Plate IV, Fig. 4.

Intermediate variety.

Neave, Trans. Ent. Soc., p. 216, pl. xii, ff. 1, 2 (1906).

Plate IV, Fig. 7.

It is only in recent years that we have had sufficient material to study these remarkable butterflies and to appreciate the relations existing between them. *P. rex* is still a rare insect, whilst *P. mimeticus* is even less frequently met with. The two forms have been regarded as separate species, but, in view of the distinctly intermediate forms described by Neave,

¹ Professor Aurivillius, in his catalogue of the African Rhopalocera, includes Moore's subgenera *Tirumala* and *Melinda* in the genus *Danaiida*, Latreille. The present work is not a systematic treatise and there-

fore I have in this case adopted the nomenclature which is in common use at the time of writing, and which is used for the most part by the writers to whose works references are given.

we must conclude that they are more closely allied than was at first supposed. That author gives some interesting facts concerning these butterflies and their models, in his paper in Trans. Ent. Soc., 1906. *P. mimeticus* is found on the west shore of Lake Victoria Nyanza. It is so rare that its range cannot be very accurately determined, but I know of no other locality where it has yet been proved to occur. In the collection described by Neave there were forty-one examples of *M. mercedonia*, of which only five were taken on the north-east shore, the remaining thirty-six coming from the north-west, and my own specimens were from the same neighbourhood. On the other hand, *P. rex* occurs on the Kikuyu Escarpment, well to the east of the lake, and fifty examples of *M. formosa* were included in the collection which the above author describes, and none of this species occurred on the west. We thus have a very close geographical correspondence between the models and their Papilionine mimics. At Nyangori the two Danaines occur together, and in this region we find the remarkable intermediate form between *rex* and *mimeticus*, the female of which is shown on Plate IV, Fig. 7. An examination of the figures will show that there is a better correspondence between the female *P. rex* and the female *M. formosa* than between their respective males, the deep ochreous basal area in the female fore-wing being larger, and the wings less angulated than in the male. The male of the intermediate form differs from typical *rex* in having the basal area of the fore-wing of an intermediate shade between the ochre yellow of *rex* and the chestnut brown of *mimeticus*. The female *mimeticus* does not greatly differ in appearance from the male. Just as there is much less difference between the sexes of *M. mercedonia* than between those of *M. formosa*, so the male and female *P. mimeticus* resemble each other more closely than do the two sexes of *P. rex*.

T. PETIVERANA AND P. LEONIDAS.

TIRUMALA PETIVERANA.

Doubleday and Hewitson (*limniace*), Gen. D. Lep., p. 93, pl. 12, f. 1 (1847).

Butler (*leonora*), Proc. Zool. Soc., p. 54 (1866).

—Lep. Exot., p. 53, pl. 20, f. 2 (1870).

Aurivillius, Rhop. Aeth., p. 33 (1908).

Plate IV, Fig. 8.

The type form of this butterfly is the *limniace* of Cramer described from an Asiatic specimen, and in that region the species has very close mimics amongst the *Papilionidae* and *Pieridae*. In Africa it has an exceedingly wide range extending from Sierra Leone to British East Africa, and as far north as Abyssinia. It is perhaps rather remarkable that a Danaine with so wide a range should not have a larger number of imitators, though the existence of more conspicuous models may in some degree explain this fact. The only pronounced mimic of the species is *P. leonidas*, though it has been suggested that the male *Euxanthe wakefeldi* is an incipient mimic.

PAPILIO LEONIDAS.

Fabricius, Ent. Syst., iii, 1, p. 35 (1793).

Staudinger, Exot. Schmet., i, p. 10, pl. 6 (1884).

Cramer (*similis*), Pap. Exot., p. 14, pl. 9, ff. B, C (1775).

Oberthür (ab. *pelopidas*), Étud. d'Ent., iv, p. 55, pl. 5, f. 1 (1879).

Aurivillius (ab. *interniplaga*), Rhop. Aeth. p. 487 (1898).

var. *brasidas*.

Felder, Verh. z. b. Ges. Wien, xiv, p. 307, &c. (1864).

Aurivillius, Rhop. Aeth., p. 487 (1898).

Plate IV, Figs. 9, 11.

Like its model *T. petiverana*, this butterfly has an extremely wide range, extending from Sierra Leone to British East Africa. It belongs to a characteristic group of *Papilios*,

one of which, *P. adamastor*, bears a very close resemblance on both surfaces to the common *Pseudacraea lucretia*. In South Africa *P. leonidas* is represented by the variety *brasidas*, which differs principally in having the spots creamy white instead of green, though in some specimens the spots in the fore-wings are fewer, smaller, and arranged in a much more *Amauris*-like pattern. The actual model of *brasidas* seems doubtful, but no doubt its general appearance suggests the pattern of several of the black pale spotted Danaines which form the models for so many African mimics. In his work on South African Butterflies, Trimen describes it as a mimic of *Amauris echeria*, and states that it settles 'precisely in the way affected by the *Amauris*, viz. on a projecting leaf or twig with the wings closed and hanging downward, and in this exposed position remaining motionless for a considerable time. On more than one occasion I have mistaken *brasidas* when so posed for *echeria*'. The variety *brasidas* would seem to be an edible species. Marshall found 'that it was promptly eaten by a mantis, a spider, and a ground hornbill'. In connexion with the mimetic tendencies of the species we have the following interesting comment by the above author (Trans. Ent. Soc., p. 507, 1902).

'I have always been struck with its (*leonidas*) marked difference in habit from the southern *brasidas*. Its flight is strong and rapid, and it always goes straight ahead like *P. policles* and *P. antheus*, which it somewhat resembles on the wing, in spite of its very different shape. *Brasidas* on the other hand, has a slow sailing flight, going backwards and forwards over the same ground, and often frequenting one spot for days. Now there is absolutely nothing suggestive of protection in the flight of *leonidas*, none of that slow sailing movement to show off its coloration, which is so characteristic of the protected Danaine and Acraeine. Moreover, there is no Danaine occurring south of the Zambesi which is anything like it at all, and this is very significant. I cannot therefore resist the conclusion that in this country *leonidas* is one of those unprotected species which has succeeded in the struggle for existence by its strong and rapid flight, and perhaps by protection in the larval stage, like *P. demodocus* and *P. corinneus*. Whereas in Natal, it has found it advantageous, owing to the abundance of *Amauris echeria*, to adapt its coloration in mimicry of that species by the reduction in size and number of the spots in the fore-wing, and the toning down of the colour from glaucous green to greenish white, accompanied by the marked change in its mode of flight . . . I believe in Central Africa it is said to mimic *T. petiverana*, and it would be most interesting to find out whether it has there assumed the Danaine flight.'¹

In this latter connexion Dr. Longstaff states (Trans. Ent. Soc., p. 638, 1908) that he observed *P. leonidas* flying slowly at the Zambesi Falls, though he did not see *T. petiverana*. And Mr. Neave, after collecting in North Rhodesia and the upper region of the Congo, informs me that *P. leonidas* does, in that region, fly slowly, and in a similar manner to *T. petiverana*, which it there accompanies.

It will be noticed that Mr. Marshall suggests that *P. leonidas* may be protected in its earlier stages, and it is interesting to note that Trimen states (S. Afr. Butt., 3, p. 216) that the pupa which is suspended on the underside of the leaves is extremely difficult to distinguish, as the outline and coloration 'all combine to assimilate the pupa to the surrounding foliage in the most deceptive manner'. *Brasidas* does not appear to have a very wide range, being largely confined to the south of Africa, Cape Colony, Zululand,

¹ The wording of this passage is purely figurative. No one, least of all Mr. Marshall, would suggest that the butterfly could voluntarily change its appearance because it 'found it advantageous' to do so.

Natal, &c. It occurs also, however, in Angola, whence the example figured was received, and in that region it takes as its model *Amauris hyalites*, described on p. 55, and shown on Plate IV, Fig. 10.¹

THE AMAURIS CENTRED ASSOCIATIONS

The genus *Amauris* is characterized for the most part by having black and white facies, though some species have the white more or less replaced by ochreous. As a large number of mimetic butterflies are modified in the direction of some species of *Amauris*, and the species themselves are, to some extent, modified by association with one another, it will be well to describe the principal forms consecutively, and afterwards to deal with the mimicking species from other genera.

AMAURIS NIAVIUS.

Linnaeus, Syst. Nat., ed. 10, p. 470 (1758).	Swinhoe, Journ. Linn. Soc. Zool., xxv, p. 343,
Clerck, Icon. Ins., pl. 32, f. 2 (1764).	pl. 17, f. 4 (1896).
Fabricius (<i>niavices</i>), Mant. Ins., ii, p. 25 (1787).	Trimen (<i>niavius</i> var.), Trans. Linn. Soc., xxvi,
var. <i>dominicanus</i> .	pp. 511, 521, pl. 42, f. 6 (1869).
Trimen, Trans. Ent. Soc., p. 323 (1879).	Aurivillius, Rhop. Aeth., p. 37 (1898).

Plate V, Fig. 1, 2.

This large and conspicuous species appears to be one of the commonest butterflies in Africa, and I have received it in large numbers in almost all collections. It extends from Sierra Leone to Natal. The southern form *dominicanus* was originally described by Trimen as a form of *niavius*, though that author afterwards gave it specific rank under the name *dominicanus*. Since that time the range of the butterfly has been more completely worked out, and there can be little doubt that the two forms are varieties of the same species, every degree of intermediate gradation being found in the neighbourhood of Lake Victoria Nyanza. It has the slow sailing flight common to protected species. Natal appears to be about the southern limit of its range. The *dominicanus* form is distinguished from the western type by the much larger extent of the white areas, *niavius* having an especially broad black border in the hind-wings. It is interesting to note that this difference is also very noticeable in the mimicking species which accompany it in its different localities.

AMAURIS OCHLEA.

- Boisduval, Voy. Deleg., ii, p. 589 (1847).
 Trimen, Rhop. Af. Aust., p. 85, pl. 2, f. 6 (1862).
 Aurivillius, Rhop. Aeth., p. 38 (1898).

Plate IV, Fig. 13.

A. ochlea is a common southern and eastern species, bearing a typical black and white *Amauris* pattern. It extends from Natal to German and British East Africa. In the former region it is variable in its occurrence, being sometimes comparatively rare. It is accompanied by several mimetic species, its closest imitator being *Hypolimnas deceptor*. The Rev. K. St. A. Rogers describes the species as being fonder of the open country and more partial to flowers than is *A. niavius*.

¹ Mr. Neave in his extensive paper on 'Zoological Collections from Northern Rhodesia and Adjacent Territories', *Lepidoptera Rhopalocera*, Proc. Zool. Soc. 1910, suggests that species of the type of *Amauris*

hyalites have been the primary model of *P. leonidas* since their translucent spots have a pale greenish appearance when the insect is on the wing.

AMAUROS PSYTTALEA.

Plötz, S. E. Z., xli, p. 189 (1880).

Brown (*enceladus* var.), Ill. Zool. p. 18, pl. 9 (1776).

Beauvois (*damocles*), Ins. Af. et Amer., p. 239, pl. 6, ff. 3a, 3b (1805-21).

Haase (*egialea*), Bibl. Zool. (8), ii, pl. 4, f. 25 (1891).

var. *damocles*.

Staudinger, Iris, viii, p. 367, pl. 7, f. 3 (1896).

Aurivillius, Rhop. Aeth., p. 37 (1898).

Plate IV, Fig. 12. Plate V, Fig. 3.

The example figured on Plate IV was received from Entebbe, but the insect has a very wide range, and occurs from Sierra Leone to German East Africa. I have examined a very long series of the species, and find that it varies considerably in the amount of white on the hind-wings, and in the size of the white spots in the fore-wings, though the relative size and position of these is fairly constant. There is, perhaps, a certain tendency for the white area of the hind-wings to be reduced as we travel westwards, though great variation occurs in the same locality. Two specimens before me as I write, taken at Toro, show extreme variation, one having very little white on the hind-wings whilst the other not only has a large white basal area extending considerably beyond the end of the cell, but has also a very prominent row of submarginal white spots. There is no difference in the markings in the two sexes. The form *damocles* is principally characterized by the large white area in the hind-wings, and any of the many varieties with a large white area may be said to approach the *damocles* form.

AMAUROS HYALITES.

Butler, Cist. Ent., i, p. 209 (1874).

Aurivillius (*difficilis*), Ent. Tidskr., xii, p. 194, 197 (1891).

Swinhoe (*egialea*), Journ. Linn. Soc. Zool., xxv, p. 343, pl. 17, f. 6 (1896).

Aurivillius, Rhop. Aeth., p. 38 (1898).

Plate IV, Fig. 10.

The *hyalites* section of the genus may be distinguished from that which includes *A. niavius* and *A. psyttalea*, by the presence in the former of a rather wavy and white speckled margin in the hind-wings. The example figured was received from Ogowe in the French Congo, though the species extends to Lake Tanganyika. A closely allied form is *A. dannfelti* Auriv., which was described from the Congo, and of which several specimens have lately been taken by Mr. Neave, near Lake Bangweolo. *A. hyalites* acts as a model for *P. brasidas*, where that insect occurs in Angola.

AMAUROS HECATE.

Butler, Proc. Zool. Soc., p. 44 (1866).

Doubleday and Hewitson (*niavius*), Gen. Di. Lep., pl. 11, f. 3 (1847).

Aurivillius, Rhop. Aeth., p. 39 (1898).

Plate IV, Fig. 14.

This species extends from Sierra Leone to West Uganda, and may be easily recognized by the peculiar shape of the wings, and the paucity of the white markings. The pattern evidently has considerable influence on certain forms of *Hypolimnas dubius*, the form *damoclina* being apparently modified in the direction of this *Amauris*. The example figured was received from Cameroon.

AMAUROS ECHERIA.

Stoll, Suppl. Cram., p. 135, pl. 29, ff. 2, 2b (1790).
 Trimen, Trans. Linn. Soc., xxvi, p. 521, pl. 42,
 f. 3 (1869).
 Godart (*vaillantina*), Enc. Meth., ix, p. 183 (1819).
 Trimen, Metamorph. S. Af. Butt., i, p. 58 (1887).

Kheil (var. *steckeri*), B. E. Z., xxxiii, p. 393, Fig.
 (text) (1889).
 E. M. Sharpe (var. *jacksoni*), Proc. Zool. Soc.,
 p. 633, pl. 48, f. 2 (1891).
 Aurivillius, Rhop. Aeth., p. 39 (1898).

Plate V, Figs. 10, 13.

AMAUROS ALBIMACULATA.

Butler, An. N. H. (4), xvi, p. 394 (1875).
 Boisduval (*echeria* var.), Voy. Deleg., ii, p. 589
 (1847).

Trimen, Trans. Linn. Soc., 26, p. 521, pl. 42,
 f. 7 (1869).
 Butler (*hanningtoni*), Proc. Zool. Soc., p. 91
 (1888).

Plate V, Fig. 4.

I have taken these two species together, in order to make a comparison between them, apart from the various species of other genera, which appear to be modified in mimetic association with their patterns. They were for a long time considered to be merely varieties of the same species, and as such were described by Trimen in his work on the South African butterflies, and also by Professor Aurivillius in his 'Rhopalocera Aethiopica'. Messrs. Rothschild and Jordan have, however, shown (Novit. Zool., 10) that they are certainly distinct species. Whilst *A. albimaculata* appears always to have white spots on the fore-wing, these marks in *A. echeria* are sometimes white and sometimes ochreous. The general appearance of the two insects is much the same, but they may be distinguished by the following differences. The sexual brand in the male *albimaculata* is longer than in *echeria*. In both sexes of *A. albimaculata* the underside of the abdomen is as pale as, or paler than, the median band of the hind-wing, whilst in *echeria* it is as dark as the marginal area of the hind-wing. In *albimaculata* the white spot on the palpus is always in the form of a streak, whilst in *echeria* it is in the form of a dot. This latter feature is perhaps the easiest to recognize at a glance, and forms a very ready means of distinguishing between the species.

Trimen describes the larva and pupa of *A. echeria* as follows :—

'Larva. Black with narrow blue and orange longitudinal stripes. Median dorsal stripe, from 5th to 13th segment, very narrow, bright blue; subdorsal lateral stripe interrupted, yellow-orange; spiracular stripe (superior) interrupted, pale-orange (inferior), festooned on each segment, yellow-orange. Spiracles faintly ringed with light blue. Skin slightly rugose. Head smooth, black. Five pairs of rather short, divergent, subdorsal black filaments, springing respectively from the 2nd, 4th, 6th, 11th, and 12th segments.

'Pupa. Thick, short, gibbous, moderately angulated. Shining silvery golden; the angles and points defined with markings of red and black, attached by tail only.'

The butterfly is described as having a slow and graceful flight, though capable of rapid movement when alarmed. It frequents the neighbourhood of woods, though fond of flying across open spaces. After examining a long series of both *echeria* and *albimaculata*, I find that both species are liable to occasional variation in the direction of a brown ground-colour in place of the usual black. A brown example of *echeria* is shown on Plate V, Fig. 10. This specimen I received from German East Africa, and on further inquiry was informed that it is not at all uncommon in that region. In *albimaculata* the discal pale patch in the hind-wing is frequently almost white, whilst in *echeria* it is always ochreous. *Echeria* extends from Cameroon to the Cape, whilst *albimaculata* seems to be centred in the Natal region, extending to North-

East Rhodesia, and to Mount Kilimanjaro, but is rare in Cape Colony. The variety *steckeri* is peculiar to Abyssinia, and has a very narrow band on the hind-wing, and numerous marginal spots, and the fore-wing spots, hind-wing patch, and other pale markings are brownish-ochreous. The variety *jacksoni* is generally larger, has a well-marked spot in the discoidal cell in the fore-wings, and the discal ochreous patch in the hind-wing is somewhat smaller in extent.

The species of *Amauris*, whilst serving as models for a large number of butterflies of other genera, are by no means exempt from the influence of their own patterns upon each other. This subject has been carefully investigated by Mr. Neave, and the results of the examination were included in his paper on 'Bionomic Notes on Butterflies from the Victoria Nyanza' (Trans. Ent. Soc., 1906). Here it was shown that both *A. echeria* and *A. albimaculata* have been modified in the Victoria Nyanza region by the presence of *Amauris psyttalea*. In that locality the specimens of *echeria* are of the *jacksoni* form, and the examples of *albimaculata* are represented by the form *hanningtoni*, Butl., in which the spot in the fore-wing cell is larger, and there is a tendency in both wings towards the appearance of more numerous submarginal spots than in the type form, a feature common to the *damocliides* form of *A. psyttalea*. The discoidal cellular spot was measured in a large number of specimens, and it was found that in South African examples of *A. echeria* the average dimensions of this marking were 2.26 mm. by 1.13 mm., whilst in *echeria f. jacksoni* these measurements became 3.73 mm. by 1.46 mm. in British East Africa, and 4.05 by 1.525 mm. to the east and north-east of Lake Victoria Nyanza, and to the west of that lake the dimensions were 3.947 mm. by 1.704 mm. Similarly southern examples of *albimaculata* averaged 2.13 mm. by 1.02 mm. in British East Africa, 3.32 mm. by 1.52 mm., north-east of the lake 3.86 mm. by 1.75 mm., and to the west 3.953 mm. by 2.232 mm. In addition to the evident modification in *echeria* and *albimaculata* it is further pointed out that *echeria* is itself modified as we proceed westwards, so that the pale marking of the hind-wings becomes reduced in area, so as to cause an approach towards *A. hecate*. Accurate research of this nature is extremely valuable and interesting, as showing with what precision selection may act in the production of Müllerian mimicry. It is not, of course, suggested that insectivorous enemies observe the exact size or even the number of the spots on a butterfly's wing. It is the general effect produced by the markings during flight which is modified by these apparently small differences, which, in view of the above facts, must be regarded as of selective value.

The example of *A. echeria* on Plate V, Fig. 13, is of the *jacksoni* form and was taken at Kilimanjaro. The fore-wing spots are much paler than in typical Natal forms, which latter are also generally somewhat smaller. The example of *albimaculata* is from Durban. It exhibits the smaller size common to the more southern specimens, and the minuteness of the fore-wing cell spot is very well illustrated.

HYPOLIMNAS DECEPTOR.

Trimen, Trans. Ent. Soc., p. 105 (1873), ♂.
 — S. Af. Butt., i, p. 286, ♂ and ♀, pl. 6, f. 3 (1887).
 Hopffer (♀ *dubia*), Peters Reise. Moss. Ins.,
 p. 385 (1862).
 Smith (var. *deludens*), An. N. H. (6), vii, p. 125
 (1891).

Smith (var. *deludens*), Rhop. Exot. 43 *Hyp.*,
 p. 6, pl. 3, ff. 3-5 (1898).
 Butler (*kirbyi*), Proc. Zool. Soc., p. 51
 (1898) ♂.
 Aurivillius, Rhop. Aeth., p. 149 (1898).

Plate IV, Fig. 17, ♀.

Trimen described both sexes of this butterfly in 1887 and gave a figure of the female. The insect described as *H. kirbyi* by Butler, in 1898, corresponds with the male of *deceptor*, as described by the former author, and as such it is now recognized. All possible question

has, however, been set at rest by the fact that Mr. Millar, at Durban, has bred a fine series of both *deceptor* and 'kirbyi' from ova, all the *deceptor* being females, and all the 'kirbyi' males. The resemblance of *deceptor* to *A. ochlea* is very striking in both sexes, and is somewhat accentuated in the female by the larger area of the white markings. The butterfly is highly iridescent,¹ and fresh specimens are exceedingly beautiful, the males having a rose-coloured sheen, whilst the females vary in different lights from blue to mauve. The species is found in Natal, Nyassaland, and British and Portuguese East Africa. It is described as not rare but difficult to obtain in good condition.

PSEUDACRAEA LUCRETIA.

Cramer, Pap. Exot., i, p. 71, pl. 45, f. c, D (1775).	var. <i>tarquinia</i> .
Fabricius (<i>sulpitia</i>), Ent. Syst., iii, 1. p. 245 (1793).	Trimen, Trans. Ent. Soc., p. 79, pl. 5, f. 3 (1868).
var. <i>expansa</i> ,	—S. Af. Butt., i, p. 289 (1887); iii, p. 404 (note) (1889).
Butler, An. N. H. (5), ii, p. 177 (1878).	var. <i>heliogenes</i> .
Trimen (<i>delagoae</i>), S. Af. Butt., i, p. 291 (1887).	Butler, An. N. H. (6), xviii, p. 69 (1896).
var. <i>protracta</i> .	Aurivillius, Synonymy, Rhop. Aeth., p. 174 (1898).
Butler, Ent. Mo. Mag., xi, p. 164 (1874).	

Plate IV, Fig. 15 (*expansa*). Plate V, Fig. 14 (*tarquinia* ♀ ab.).

Of the varieties of this *Pseudacraea* enumerated above, several, in the absence of long series for comparison, have been described as separate species. Professor Aurivillius, however, regards them as all forms of the original *lucretia* of Cramer. The species is very common, and I have received it in considerable numbers from various localities. In one form or another it extends from Sierra Leone to Natal. In no form can it be considered as a close mimic of any dominant species, though its general black and white appearance suggests various species of *Amauris*, whilst the varieties with black and white markings approach *A. echeria*. The *lucretia* form resembles Plate IV, Fig. 15, but the white areas are more restricted and clearly defined, whilst the ground-colour is richer. In the *protracta* variety the pale markings are all more or less ochreous, and darker in the hind-wing. In *tarquinia* the sub-apical white markings are smaller and more separated, and in the female the pale discal area of the hind-wings is ochreous. Sometimes the spots of the fore-wings are also ochreous, and in one specimen I have seen all the markings are of that colour. On Plate V, Fig. 14, I have illustrated a peculiar aberration of the female from my own collection, not because it is a good instance of mimicry, but because it appears to illustrate the limit of variation in the female. Some forty-five examples are before me as I write, and one specimen from Natal comes very near to the above variety, though the hind-wings are nearly white. The remainder present every gradation from this form to an example from North-East Rhodesia, in which the hind-wings are nearly all white, having only a narrow brown margin, and the white bar in the fore-wings is broad and continuous, extending from just below the costa to the posterior angle, where it is nearly joined by the inner-marginal patch. The well-known Planemoid aposeme, viz. the brown, black-spotted basal patch on the underside of the hind-wing, is very conspicuous. It may be noted here that the West African *Papilio adamastor* appears to be synposematic with *Ps. lucretia*. From this fact and its great abundance, I am inclined to regard this *Pseudacraea* as a Müllerian mimic.

¹ This iridescence is much brighter in the ♀ than in the ♂, a circumstance unusual in butterflies.

PAPILIO ECHERIOIDES.

Trimen, Trans. Ent. Soc., p. 72, pl. 6, ff. 1, 2 (1868).

Aurivillius, Rhop. Aeth., p. 468 (1898).

Plate V, Fig. 7, ♀.

The example figured on Plate V was taken near Dar-es-Salaam, in German East Africa, and differs somewhat in appearance from the average specimen owing to the comparative whiteness of the discal patch on the hind-wing, which gives the insect a close resemblance to *A. psyttalea f. damocles*, the example of which, also figured on Plate V, was taken in the same neighbourhood. Many examples of the female have an ochreous patch on the hind-wing, and thus resemble *A. albigulata* and the white-spotted forms of *A. echeria*. After a careful examination of the females of *P. echerioides* and *P. homeyeri* I can find no very certain method of distinguishing between them. The key to the species provided in Professor Aurivillius's catalogue does not supply any clear marks of distinction. The only special feature of the female *P. homeyeri* therein mentioned is the fact that in that species there is no submarginal spot above the fore-wing upper radial, and as this is equally the case in *echerioides* it does not afford any assistance. The specific distinction between the three forms *echerioides*, *homeyeri*, and *jacksoni* is extremely small. The genitalia, which are usually appealed to in difficult cases, do not in this instance afford assistance, as they are practically alike in the three species (see Novit. Zool., xii, p. 185, 1905). It is only in the males that any marked difference is to be observed. The male *P. echerioides* is black. The fore-wing has minute white dots on the margin in the internervular spaces. There is a submarginal row of eight creamy white spots, of which the second is the smallest, the first and third about the same size, and the remainder increasing in length towards the inner-margin. The seventh is doubled, and the eighth is a streak. The hind-wing has a narrow white discal band and a submarginal row of six white spots (much nearer to margin than in *jacksoni* and *homeyeri*), and small white marks on the margin in the internervular spaces. The butterfly ranges from the Cape to German East Africa. Trimen records (S. Afr. Butt.) that he mistook the first two females he saw for *P. dardanus cenea* ♀ *f. cenea*, and that they hovered flutteringly near the ground whilst the males coursed rather rapidly and irregularly over the underwood.

PAPILIO JACKSONI.

E. M. Sharpe, Proc. Zool. Soc., p. 188, pl. 17, ff. 1, 2 (1891).

Aurivillius, Rhop. Aeth., p. 468 (1898).

Plate V, Fig. 8, ♀.

With *P. cynorta*, *P. homeyeri*, and *P. echerioides*, this butterfly belongs to a group in which the males are characterized by a black ground-colour with transverse white markings, whilst the females are all greatly modified in the direction of Danaine or Acraeinae models. The male *P. jacksoni* is black, with a submarginal row of eight pure white spots in the fore-wing, running parallel to the hind-margin. The second of these, above the upper radial, is the smallest, and the remainder increase gradually in length towards the inner-margin, where they are almost half as wide as in *homeyeri*. The spot below the first median is doubled, the two halves contiguous in the centre, and the eighth spot is on the inner-margin. From a little beyond the middle of the costa of the hind-wing to a point rather above the middle of the inner-margin, extends a white bar rather more curved on the distal than on the basal side. A row of six submarginal white spots (separated from margin more widely than in *echerioides*), and small white spots on the margin between the extremities of the nervules in both wings. On the hind-wing underside the basal area is red-brown with one

round and one linear black spot below the costal, three black streaks in the cell, and one below the median. There is a white spot in the fore-wing cell at the point where the subcostal bends downwards. As will be seen from the figure, the female is greatly modified in the direction of the white-spotted forms of *A. echeria*. The species occurs in British and German East Africa, Kikuyu, and Ruwenzori region.

PAPILIO HOMEYERI.

Plötz, Stet. Ent. Zeit., xli, p. 306 (1880).

Karsch (*neumanni*), Ent. Nachr., xxi, p. 225 (1895).

Oberthür (*tanganikae*), Bull. Ent. Fr., p. 190, ff. 8, 9 (1897).

Aurivillius, Rhop. Aeth., p. 469 (1898).

Plate V, Fig. 11, ♀.

The female of this *Papilio* is not easy to distinguish from that of *P. jacksoni*. The male has the submarginal white spots in the fore-wing much larger, and the cell spot is visible on the upperside. There is also an indistinct whitish streak just below the origin of the last two subcostal branches. Judging from the examples I have examined, the most constant difference between the females is the usually browner ground-colour in *homeyeri*, in which respect it corresponds to the brown form of *A. echeria*. The species extends further west than *jacksoni*. The specimen figured was received from German East Africa, but it is also found in Angola. The female *P. homeyeri* is a very perfect mimic of *A. echeria*. There is no better illustration of the attractive force of this *Amauris* and its ally *A. albimaculata* than the examination of a collection showing the Danaine species, together with *P. jacksoni*, *P. homeyeri*, *P. dardanus cenea* ♀ *f. cenea*, *H. dubius f. mima*, and *H. dinarcha*, together with some of the more ochreous-tinted specimens of *P. echerioides*. For various reasons these species have not been thus grouped together on the plates in the present work, but an examination of the figures will give an idea of the close resemblance which obtains between the forms named.¹ The male *P. homeyeri* is black. The fore-wings have usually eight and sometimes only seven white spots arranged in a broad submarginal gradually widening band, parallel to the hind-margin. The second spot is the smallest (sometimes absent), the seventh is very large and wide (twice as wide as in *jacksoni*), and is separated from the eighth or inner-marginal spot only by the submedian nervure. There is a small white horizontal mark near the end of the cell, and another, usually larger, beyond the cell and above the upper radial. The hind-wings have a discal white band about twice the width of that in *P. echerioides*, and there is a submarginal row of small white spots sometimes obsolescent, and placed very much nearer to the margin than the corresponding spots in *P. echerioides*. The red-brown basal area of the hind-wing underside is smaller than in *P. echerioides*. There is one round and one linear black spot above the subcostal, three black lines in the cell and one below the median.

The foregoing species of *Papilio* are undoubtedly very closely allied, the comparative lack of any characteristic distinction between the females being very remarkable.

There are two other butterflies of this group of *Papilios*, viz. *P. zoroastres*, Druce, and *P. preussius*, Karsch. Of the latter I have examined the original figures and there appears to be little to distinguish the male from that of *P. homeyeri*, whilst the female might be either that species or *P. echerioides*. The spots on the fore-wing are said to be yellowish rather than white. *P. zoroastres* was described from a male, and I have not been able to find a specimen or description of the female.

¹ Lack of space has prevented a figure of *H. dinarcha* being included, see pp. 63 and 64.

HYPOLIMNAS DUBIUS.

- P. de Beauvois, *Ins. Afr. et Amer.*, p. 238, pl. 6, f. 2a, 2b (1805).
- var. *cerberus*.
Aurivillius, *Ent. Tidskr.*, xv, p. 281 (1894).
— *Metamorph.*, l. c., p. 282, pl. 4, f. 4, 4a, 4b (1894).
- var. *damoclina*.
Trimen, *Trans. Linn. Soc.*, xxvi, p. 505 (note) (1869).
- var. *mima*.
Trimen, l. c., p. 506 (note), pl. 43, f. 7 (1869).
— *S. Af. Butt.*, i, p. 284 (1887).
- var. *drucei*.
Butler, *Trans. Ent. Soc.*, p. 426, pl. 6, f. 3 (1874).
Boisduval (*dubius*), *Faune. Mad.*, p. 40 (1833).
Mabille (*lutescens*), *Hist. Mad. Lep.*, i, p. 162, pl. 18, ff. 8, 9 (1885-7).
- ab. *bewsheri*.
Butler, *An. N. H.* (5), iii, p. 187 (1879).
Mabille (*drucei*), *Hist. Mad. Lep.*, i, p. 160, pl. 18a, ff. 5, 6 (1885-7).
- var. *anthedon*.
Doubleday, *An. N. H.*, xvi, p. 181 (1845).
— *Gen. D. Lep.*, pl. 37, f. 2 (1850).
- var. *wahlbergi*.
Wallengren, *Rhop. Caffr.*, p. 27 (1857).
Trimen, *S. Af. Butt.*, i, p. 282, pl. 6, f. 2 (1887).
— (*anthedon*), *Rhop. Af. Austr.*, p. 152 (1862).
— *Trans. Linn. Soc.*, xxvi, p. 511 (note) (1869).
Butler (*marginalis*), *An. N. H.* (4), xvi, p. 395 (1875).
Swinhoe, *Journ. Linn. Soc.*, xxv, p. 343, pl. 17, f. 3 (1896).
Weymer (*angustolimbata*), *S. E. Z.*, liii, p. 87 (1892).
Mabille (var. *madagascariensis*), *An. E. Belg.* 25 Bull., p. 55 (1881).
— *Hist. Mad. Lep.*, i, p. 158, pl. 20a, f. 2 (1887).
Aurivillius, *Synonymy, Rhop. Aeth.*, pp. 149, 150, 151 (1898).

Plate IV, Fig. 18. Plate V, Figs. 5, 6, 12, 15.

Hypolimnas dubius presents one of the most curious and complicated instances of polymorphism yet discovered. In most other species which exhibit this feature the phenomenon is confined to the female, except in cases of seasonal dimorphism, and in the peculiar case of *Charaxes neanthes* and *Ch. zoolina*, which are now found to be two forms of the same species. Previously to Millar's breeding experiments *H. dubius* was known to be extremely variable and to produce some six more or less marked varieties. Fig. 15, Plate V, may be taken as nearest to the type form, whilst Fig. 18, Plate IV, is nearest to the form *damoclina*, Trimen. The specimen I have figured is somewhat unusual in having the pale basal area of the hind-wing yellowish instead of white, which latter, from an examination of a number of examples, appears to be the more usual colour, as indeed we should expect, since the variety is evidently modified in the direction of *Amauris hecate*. The form *mima*, Plate V, Fig. 12, is less modified than other varieties, the principal change being the substitution of yellow for white in the hind-wings, and this, combined with the reduction in size of the white spots in both wings, produces a very close approach to *Amauris albimaculata* and the white spotted forms of *A. echeria*. The variety *cerberus* of Aurivillius is characterized by the absence of white in the hind-wing, thus mimicking *A. tartarea*, Mab., a species somewhat resembling *A. hecate*, but larger and without the white hind-wing basal area. The varieties *drucei* and *bewsheri* are Madagascar forms not greatly differing in appearance from the type. The form *anthedon* of the west is represented in the east and south by *wahlbergi*, which with its brilliant iridescence is one of the most beautiful of African insects. It will be noticed that *anthedon*, with its broadly suffused dark border in the hind-wing, is modified in the direction of *A. niavius*, whilst the southern *wahlbergi*, with its narrow black margin, mimics the *dominicanus* form of the Danaine model. It was in 1897 that Marshall, writing to Professor Poulton (*Trans. Ent. Soc.*, p. 491, 1902), expressed the opinion that *mima* and *wahlbergi* were two forms of the same species. He says, 'In my own mind I am pretty well convinced that *Euralia mima* and *wahlbergi* are one and the same species which has developed two mimetic forms as in *Papilio*

cenea, but that in this case both sexes are concerned. My reasons for so thinking are that they have been taken *in coitu* several times, that specimens occur presenting intermediate coloration, and also that the two forms are always found together whenever they are met with in any number. I have not often been fortunate enough to see these congregations, but I remember seeing some thirty or forty specimens, comprising about equal numbers of each form, collected together on the side of a steep shady kraantz along the Palmiet River. Mr. A. D. Millar, who has collected for many years in Durban, tells me this is by no means uncommon, and that they congregate particularly in the afternoon when going to roost. Mr. C. N. Barker tells me that some years ago he came across a large number of both forms on a large tree on which they had evidently bred,¹ for many of them had only just emerged, and some had not their wings fully developed. This shows that they are also associated in their early stages.'

The same writer subsequently had no opportunity of pursuing the investigation, and some years were destined to elapse before proof of the species identity of the forms could be obtained by breeding. At the meeting of the Entomological Society of London, in April 1910, Professor Poulton read a preliminary note communicated by Trimen, 'on Mr. A. D. Millar's experimental breeding of forms of the Nymphaline genus *Euralia*'.² The facts then disclosed were as follows:—

1. Ten ova from an example of *wahlbergi* produced two males, one female, and one deformed individual of the parent type, and also four males and one female *mima*.
2. Thirty-nine ova from an example of *mima* produced thirty-three imagines, twenty-four males and nine females, all of which were of the parent type.
3. Eleven ova from an example of *mima* produced eight of the parent type, five males and three females, and three *wahlbergi*, all males.

None of the examples resulting from the above experiments shows any departure from the respective type.

Beyond the establishment of the species identity of the two forms *mima* and *wahlbergi* it would perhaps be premature to discuss the results of these experiments. It was pointed out in the communication referred to that in spite of the result of the investigation *mima* is apparently the rarer of the two forms in Natal, a consideration which, if absolutely correct, would preclude an explanation similar to that suggested for the dominant condition in that region of the *cenea* form of *P. dardanus*. Professor Poulton at the same time suggested that the two forms might be regarded as a Mendelian pair.³ He also exhibited six examples of *anthedon* and four of *dubius* taken in the same locality near Lagos in 1909, pointing out that by analogy with the eastern forms *mima* and *wahlbergi*, their western representatives might with confidence be regarded as specifically identical.

The meaning of these polymorphic forms is very obscure. On the theory of mimicry we should expect a mimetic butterfly to have developed an approach to that model the pattern of which afforded the best protection. On Müllerian grounds the tendency must

¹ This assumption must now be corrected in view of the fact that Millar's experiments show that the food plant is a species of nettle (*Fleurya*, sp.?).

² Aurivillius includes *Euralia* in *Hypolimnas*.

³ I have not in the present work attempted to deal with the subject of Mendelism. Even were I qualified by a special knowledge of Mendelian principles to

discuss their bearing on the present subject, I should hardly deem the time ripe for such an effort. The intricacies of Mendelian heredity are being carefully studied by scientists well qualified for the investigation, and their bearing, if any, on the phenomena of mimicry will doubtless be duly discussed when adequate data become available.

always be towards a reduction in the number of warning patterns, and this is what we do actually find in unquestionably Müllerian associations. We are forced, therefore, to the conclusion that species which in the same locality produce polymorphic mimetic forms, are Batesian mimics, and that the value of the multiple varieties lies in the distribution of the mimetic forms amongst a corresponding number of models, thus avoiding the risk of the edible mimic becoming more numerous than its distasteful model, a state of things which would lead to a disastrous increase in the amount of experimental tasting by insectivorous animals. Indeed, we may suppose that this process has actually taken place, and that under its influence the same species has developed new mimetic forms, thus causing such phenomena of polymorphism as we now observe in the case of *H. dubius*. The obscure and complicated processes by which a female butterfly can produce ova which give rise to several forms belong to a separate study. That they do so is an established fact, of which the only feature affecting the present consideration is that when these differing forms are produced they are not promiscuously coloured, but in nearly every case resemble common distasteful species of other genera.

Professor Aurivillius thus describes the larva and pupa of *dubius* from specimens obtained in the Cameroon (Ent. Tidskr., p. 282, 1894):—

‘The larva is black, and has at each of the segments 1–11 a narrow white transverse band, from which arise the dorsal and lateral spines. The head is pale and bears two long spines. The first segment has two lateral but no dorsal spines; and in the remaining segments the spines are arranged as in the larva of *Salamis anacardii*. The spines are pale at the base and darker towards the end. Legs light coloured.

‘The pupa is brown speckled with black, and has a short black cremaster. Dorsal spines short.’

As the arrangement of the spines in the larva is compared to that in *S. anacardii*, I append the description of these also:—

‘Second and third segment on each side with two spines placed close together, the fourth with two spines placed one above the other, and the fifth with three sublateral spines. There are also two sublateral spines at the tenth segment, the lower of which, however, is very small; the remaining segments have, on the contrary, no sublateral spines. The twelfth segment appears to have only two spines, in that the dorsal spine is so far removed forward that it appears to arise from the eleventh.’

I have examined a long series of about seventy examples of *H. dubius*. Of these, twenty-three were typical *wahlbergi* from Natal, Zululand, and British East Africa. They varied little beyond the fact that the Natal specimens generally, though not always, had a narrower sub-apical bar on the fore-wing. Nine were of the *mima* form from Natal and Zululand, varying only in the extent of the yellow patch in the hind-wing and the size of the white spots on the primaries. Fourteen *anthedon* from Sierra Leone to Lake Tanganyika showed some variation in the width of the black hind-wing border, always, however, much broader than in *wahlbergi*. The remaining examples varied from typical *dubius*, through *damoclina* to *cerberus*, the last having the hind-wings entirely black. In this form it is very remarkable that whilst the white of the hind-wings has disappeared, the cell spot in the fore-wing remains large, larger than in many examples even of *dubius*, thus increasing the resemblance to the model *A. tartarea*.

There is one other African *Hypolimnas* allied to *H. dubius* which is a member of the *echeria* association, viz. *H. dinarcha*, Hew., which occurs from Sierra Leone to British East Africa. It is nearly as large as *H. usambara*, but resembles white-spotted *echeria* in colour

and pattern. In a note in Roger's paper in Trans. Ent. Soc., 1908, Professor Poulton observes that *H. dinarcha* occurs in the central part of the Congo State as the variety *bartteloti*, Grose Smith, and that whilst *A. echeria* and *A. albimaculata* do not occur there, the model is supplied by a form of *Amauris egialea* having an ochreous hind-wing patch. The point is extremely interesting as showing how a species may extend its range by following a slightly different model, a process which might be carried on for a long period, the mimicking species ultimately resembling a very different model from that which first attracted it from its ancestral pattern.

HYPOLIMNAS USAMBARA.

Ward, Ent. Mo. Mag., ix, p. 148 (1872).

Staudinger (*imperialis*), Exot. Schmet., i, p. 137, pl. 47 (1885-6).

Aurivillius, Rhop. Aeth., p. 151 (1898).

Plate V, Fig. 9.

This magnificent species is one of the largest and rarest of the genus *Hypolimnas*. Except for the reddish patch at the anal angle of the hind-wing, it might be almost taken for an exceptionally large example of *H. wahlbergi*, though the absence of the white spot in the fore-wing cell, and the presence of the red-brown areas on the underside are very distinctive. It is marked on the underside as on the upper, but the apical area between the white bar and the margin is reddish-ochreous, and in the hind-wing there is a submarginal bar of the same colour, the margin being narrowly bordered with black, ornamented with white spots dusted with blue. The butterfly forms another member of the group mimetically associated with *A. niavius dominicanus*. The example figured was taken near Rabai. The Rev. K. St. A. Rogers in regard to this species writes as follows (Trans. Ent. Soc., p. 497, 1908): 'I have taken two more specimens of *Euralia usambara* a week ago. I must confess that the first took me in completely. It was hovering over the end of a branch in the manner of the *Amauris* model, for which I mistook it, and was just considering whether I should catch it for my spiders, when it settled and I saw what it was.'

The species appears to be restricted to German and British East Africa.

ATERICA GALENE.

Brown, New Ill. Zool., p. 94, pl. 37 (1776).

Cramer (*cupavia*), Pap. Exot., iii, p. 2, pl. 193, ff. E, F (1779).

Hopffer (var. *theophane*), Sitz. Akad. Wiss. Berlin, p. 641 (1855).

— Peters, Reise Mossamb. Ins., p. 387, pl. 22, ff. 7-10 (1862).

Aurivillius, Rhop. Aeth., p. 180 (1898).

Plate IV, Fig. 16.

This butterfly has a very wide range extending from Sierra Leone to German East Africa, and is rather variable in appearance. The example figured was received from Entebbe, together with the *Amauris psyttalea* which I have figured on the same plate. The male is smaller and has much more black on the hind-wings, whilst all the spots and markings are pale yellow. I have examined a large series of this butterfly from West Africa, and find that the females in that region usually have a fairly well-marked double line of pale submarginal crescentic markings in the hind-wing, whilst there is often a reddish-brown suffusion extending from just within this border, nearly to the end of the cell. Occasionally a form of the female appears in which the spots of the fore-wing are pale yellow, whilst the discal area of the hind-wings is rich ochreous. There is a marked difference in the female example from Entebbe shown on Plate IV and the usual West African females, the discal spots in the fore-wing being larger and more confluent, thus presenting a nearer approach to the *Amauris*.

Why this should take place more particularly in East Africa is not very clear, and it would be idle to speculate on the causes, doubtless very complicated, which tend to a better mimetic development in the east than in the west. In spite, however, of their inferior mimetic development the western specimens are quite sufficiently *Amauris*-like to benefit by the resemblance, and it may be that they show an early stage of the development which has become more perfect in the Entebbe region.

MELINDA MORGENI.

Honrath (*Elsa morgeni*), B. E. Z., xxxvi, p. 436, pl. 15, f. 5 (1892).

Karsch, Ent. Nachr., xx, p. 228 (1894).

Aurivillius, Rhop. Aeth., p. 33 (1898).

Plate IV, Fig. 19.

I am indebted to my friend Dr. Jordan for permission to figure this extraordinary butterfly from an example in the Tring Museum. The specimen figured was taken in Cameroon. As will be seen, the insect resembles an *Amauris*, coming perhaps nearest to *A. hecate*. There is a slight chestnut-brown suffusion in the basal area of the fore-wings which is strongly reminiscent of the ground-colour of *M. mercedonia*. On the underside this chestnut-brown is much more extensive, and reaches nearly to the end of the discoidal cell, and between the submedian and first median it extends to the hind-margin. The precostal area of the hind-wing is also of the same reddish colour. It is noticeable that this presumably ancestral colour is principally found on that area of the underside which is hidden by the hind-wings when the insect is at rest. In this position the butterfly is not distinguishable from an *Amauris*. It may, I think, be regarded as a development from an ancestor common to it and to *M. mercedonia*, as a careful comparison with Fig. 3 on the same plate will tend to suggest. The marginal spots in the hind-wing have disappeared, as have most of those of the submarginal band. The spots above the first median and in the cell are much enlarged, otherwise the insects are very similar except in the ground-colour. It is apparently a very rare species, and the specimens at Tring are the only examples which I have had an opportunity of examining.

P. CONSANGUINEA AND P. FULVARIA.

PSEUDACRAEA FULVARIA.

Butler, Cist. Ent., i, p. 214 (1874).

Aurivillius, Rhop. Aeth., p. 177 (1898).

Plate V, Fig. 19 ♂.

I refer the specimen figured on Plate V with some doubt to this species. There are several West African *Pseudacraeas* which, whilst differing slightly in small details, are apparently very closely allied. The peculiarity of the example figured is that the reddish bar in the fore-wings is nearly straight, whereas in the type of *P. fulvaria* it is somewhat angulated. In other respects the specimen agrees well with the type. The female is described by Butler as having a 'broad creamy band from costal nervure to just below second median branch where it becomes obsolete, but is represented by a greyish nebula on centre of first median branch, and reappears as a creamy-ochreous patch on inner-margin; secondaries with the base greyish-ochreous, black-spotted; a central diffused creamy band from costa to inner-margin, which is ochreous'. The same author makes the suggestion that the species mimics the two sexes of *Planema formosa*, but this is an error, as the male of the latter has a narrow white discal band in the hind-wings. I have shown at Fig. 18 a male *Planema* which I received at the same time from the Gold Coast, and which would certainly appear

to be the model of the *Pseudacraea*. This *Planema* agrees for the most part with *P. consanguinea*, Auriv., in which the sexes are, however, similar. Further collections from West Africa may serve to elucidate the mimetic relations of these *Pseudacraeas* and *Planemas*. Meanwhile the question as to which species of the latter acts as the special model of the former is not vital to the general principle, since all these *Pseudacraeas* have a Planemoid appearance.

THE ACRAEA EGINA GROUP.

ACRAEA EGINA.

Cramer, Pap. Exot., i, p. 64, pl. 39, f. F, G (1775).	var. <i>areca</i> .
Herbst (<i>rudolphina</i>), Naturs. Schmet., v, p. 7, pl. 81, ff. 1, 2 (1792).	Mabille, An. E. Fr. (6), 8 Bull., p. 169 (1888).
Fabricius (<i>persephone</i>), Ent. Syst. (3), i, p. 174 (1793).	Butler (♀), Proc. Zool. Soc., 1893, p. 658 (1894).
Godart (<i>zidora</i>), Enc. Meth., ix, p. 237 (1819)	Smith (<i>khara</i>), An. N. H. (6), iii, p. 128 (1889).
[♂ only.] See note under <i>P. ridleyanus</i> .	Fig. Rhop. Exot., <i>Acraea</i> 2, ff. 1, 2 (1889).
	Aurivillius, Synonymy, Rhop. Aeth., p. 92 (1898).

Plate VI, Fig. 1 ♂; Fig. 2 ♀.

This beautiful *Acraea*, like many other species, was at first considered purely West African, but is now known to extend to East Africa. I have received large numbers from Entebbe, where it would appear to be very common, and with it came many examples of *Papilio ridleyanus*. In collections the male is seldom seen in the splendour of its original colouring, as the rich crimson rather rapidly fades after death to a brick-red,¹ an unfortunate quality which is, curiously enough, a feature of the same colour in its mimics. In some specimens there is a marked suffusion of red in the internervular spaces of the fore-wing, a variation which so far I have only observed in East African specimens. The female is a very dingy butterfly, though some examples are more brightly coloured than the figure on Plate VI. One example I have seen from Lagos has distinctly red hind-wings, whilst a specimen from Nyangori has both wings suffused with red and a well-marked whitish sub-apical bar in the fore-wings, being thus intermediate to the variety *areca*. In this eastern form the male has the whole of the ground-colour a paler red than in *A. egina*, the basal black is much reduced, and the insect generally is somewhat larger. The female has all the spots very black and distinct, the ground-colour is pale reddish-ochreous, and there is a prominent white sub-apical bar, sharply defined inwardly but suffused towards the apex. The male *A. egina* bears a considerable superficial resemblance to *Acraea perenna*, Doubl., though the latter is at once distinguished by the very marked concavity of the fore-wing hind-margin, and by the decreased width of the fore-wing.

ACRAEA ZETES.

Linnaeus, Syst. Nat., ed. 10, p. 487 (1758).	var. <i>acara</i> .
Clerck, Icon. Ins., ii, pl. 43, f. 1 (1764).	Hewitson, Exot. Butt., <i>Acraea</i> , pl. 3, ff. 19, 20 (1865).
Drury (<i>menippe</i>), Ill. Exot. Ins., iii, pl. 13, ff. 3, 4 (1782).	Trimen (<i>zetes</i>), Trans. Linn. Soc., xxvi, p. 517, pl. 42, ff. 8, 9 (1869).
Hubner (<i>mycenaee</i>), Verz., p. 27 (1816).	Felder (<i>caffra</i>), Reise Nov. Lep., p. 369, pl. 46, ff. 10, 11 (1865).
Godart (<i>zethea</i>), Enc. Meth., ix, p. 236 (1819).	ab. <i>pseudolycia</i> .
Staudinger (<i>zethes</i>) Exot. Schmet., i, p. 83 (1885).	Butler, Cist. Ent., i, p. 213 (1874).
ab. <i>jalema</i> .	Aurivillius, Synonymy, Rhop. Aeth., p. 90 (1898).
Godart, Enc. Meth., ix, p. 234 (1819).	

Plate VI, Fig. 3 ♂; Fig. 6 ♀ (*acara*).

¹ This fading is characteristic of all the *Acraeas*, showing that the red must be purely a pigment colour.

It is necessary here to mention this species of *Acraea*, since it has sometimes been considered to be the model of *Pseudacraea boisduvali*, and in its variety *acara* it is undoubtedly the model of the *trimeni* variety of that species. It is a very variable insect. West coast examples of the male are not unlike *A. egina*, though the fore-wings are brown rather than black and have little or no red marking. There is a fairly persistent but variable and suffused white sub-apical bar in the fore-wings. The female is very like that of *A. egina*. Passing eastwards the red colour gradually gains on the brown, whilst the pale sub-apical bar develops into a prominent rich ochreous patch, producing the variety *acara*. This variety frequently has a white suffusion in the discal area of the hind-wings. The male example shown at Fig. 3, Plate VI, is unusually small, the majority of the specimens being nearly as large as the female shown at Fig. 6. The rich ochreous apical patch is always a prominent feature in the *acara* form. The typical *A. zetes* is essentially western. Various intermediate forms are found at Lake Victoria Nyanza, and *acara* is commonly found in Natal.

Trimen thus describes the larva and pupa of *acara* (S. Af. Butt. i. p. 160) :—

‘Larva. Ochreous-yellow. Each segment broadly banded transversely with purplish-red, the band occupying the middle portion. Spines long and distinctly branched, blackish, springing from tubercles situated in the purplish-red bands; the two dorsal spines on segment next head longer than the rest, erect. Head ochreous-yellow. Legs and prolegs purplish-red. Feeds on *Passiflora*.

‘Pupa. Pinkish-white. Margins of head, limbs, and wing-nervures defined with black. Abdominal rows of spots arranged as in pupae of *A. horta* and *A. serena*, but more continuous; the spots rose-pink in wide black contiguous rings. Median line of underside of abdomen tinged with rose-pink; two spots of the same colour on median line of back of thorax, and one at base of wings. Head ochreous-yellow.’

Professor Aurivillius has described the larva and pupa of the western *zetes*, and I give the account here for purposes of comparison (Ent. Tidskr. p. 276. 1893) :—

‘The larva is reddish-yellow, with red shiny head, and dark transverse line on each segment above the middle. The spines are quite black and arise from disk-like shiny black tubercles. The two dorsal spines of the first segment are somewhat elongated, the remainder curved slightly backwards.

‘The pupa is yellowish with black wing-nervures, black marks on the head, a black band on the back of the thorax, traversed by two pale longitudinal lines, and five black lines, adorned with pale spots on the abdomen. The pale spots of the four posterior lines are somewhat excrescent.’

The author remarks on the similarity between this larva and that described by Trimen.

PSEUDACRAEA BOISDUVALI.

Doubleday, An. N. H., xvi, p. 180 (1845).

— Gen. Di. Lep., p. 281, pl. 37, f. 3 (1850).

Butler (var. *colvillei*), An. N. H. (5), xiv, p. 123 (1884).

Karsch (ab *deficiens*), Ent. Nachr., xxiii, p. 372 (1897).

Butler (var. *trimeni*), Ent. Mo. Mag., xi, p. 57 (1874).

Trimen, S. Af. Butt., i, p. 296 (1887).

— (*boisduvali* var.), Trans. Linn. Soc., xxvi, p. 517, pl. 43, ff. 8, 9 (1869).

Aurivillius, Synonymy, Rhop. Aeth., p. 175 (1898).

Plate VI, Figs. 4, 5, 8, 9, 10.

This is one of the most beautiful of the species of *Pseudacraea*. The resemblance of the western form to *Acraea egina* is a peculiar one, inasmuch as it is one of the few cases in which the male is a more perfect mimic than the female. As stated under the description

of *A. egina*, the female of that species is somewhat variable, and in some cases there is much more red in the hind-wings than in the example figured. Nevertheless when placed side by side the male *Pseudacraea* approaches much more nearly to the corresponding sex of the *Acraea* than does the female. A perusal of the instances of mimicry given in these pages will show that in very many cases the females only of mimicking species exhibit that tendency to variation which results in the development of a mimetic pattern, whilst in other cases both sexes are mimetic, but in all cases the female mimicry is at least as good as, and often much better than, that of the male. Only careful observation of the habits of *P. boisduvali* will furnish an explanation of its exceptional case. The mimicry is rather better on the under-side. Probably the female, as usual in many species, is more retiring in its habits and frequents wooded regions in company with the female model, in which case a rough approximation to the pattern of the latter may be a sufficiently effective protection. We have, however, additional proof of the mimetic tendencies of this *Pseudacraea* in the fact that in the east and south it becomes modified to the variety *trimeni*, and here it accompanies the variety *acara* of *Acraea zetes*. Here the mimicry is still more perfect. Just as the form *acara* frequently has a white suffusion in the discal area of the hind-wings, so *P. boisduvali trimeni* develops a similar white suffusion. The white hind-winged example of *A. zetes acara* shown on Plate VI was drawn from a single example in my own collection, but since I have had the opportunity of examining a large series of this butterfly I find that the specimen is unusually small, the average size more nearly approximating to that of the female shown at Fig. 6. In Trans. Ent. Soc., 1908, p. 552, Trimen described a form from Rabai near Mombasa which is distinctly intermediate between *trimeni* and *boisduvali*, the deep ochreous apical patch in the fore-wing being reduced to a mere streak. The original form *boisduvali* extends along the west coast from Sierra Leone to Ogowe, whilst *trimeni* is found from Natal to Mombasa and inland to Taveta.

With reference to the habits of *trimeni* there is an interesting note by Mr. Marshall quoted by Professor Poulton in Trans. Ent. Soc., 1902, p. 504, which is as follows: 'I feel quite satisfied that *Pseudacraea trimeni* is a mimetic and not a protected species. In spite of its larger size it looks wonderfully like *Acraea acara* on the wing, and the first few examples I caught completely took me in. Their flight is like that of all *Pseudacraeas* and *Euralias*—slow and sailing—so long as they are not disturbed; but if struck at and missed they are off like a shot, and do not often give one a second chance. At this particular spot (Malvern) they are a good deal commoner than *A. acara*, which is only a rare visitor. The latter is, however, common on the immediate coast, where *P. trimeni* is, I am told, pretty plentiful in good seasons.' The Rev. K. St. A. Rogers has also given us some interesting particulars in connexion with this butterfly in Trans. Ent. Soc., 1908. He there describes *P. trimeni* as common at Rabai, often indeed commoner than the *Acraeinae* models. It is found in the same situations as the *Acraeas*, though the flight is described as being more lofty and sustained, and the insect is liable to fly rapidly when alarmed. It is evident that this author is inclined to regard the mimicry as Müllerian, as he points out that 'the integuments of the thorax are very tough and quite different from those of species which adopt a protective (cryptic) appearance'.¹

¹ It may be well at this point to call attention to the resemblance of the underside of the great *Papilio antimachus*, Dru., to that of *Pseudacraea boisduvali*. The upperside of the former butterfly also has the appearance of a gigantic *Acraea*. We have in this

case the difficulty of the great disparity in size between *antimachus* and even the largest of the red and black-spotted *Acraeas*. It is probable, however, that further acquaintance with the habits and localities of the species will show that the resemblance is not

PAPILIO RIDLEYANUS.

White, An. N. H., xii, p. 262, f. p. 264 (1843).

Doubleday, Hew. and Westw., Gen. Di. Lep., p. 8, pl. 3, f. 3 (1846).

Aurivillius, Synonymy, Rhop. Aeth., p. 479 (1898).

Plate VI, Fig. 7, ♂.

This species is somewhat widely distributed in Africa, extending from the west coast to Lake Victoria Nyanza, and I have received it in considerable numbers from Entebbe, taken with *Acraea egina* at the same time and place. The female is rare in collections. It differs from the male in having much more rounded fore-wings, the dark areas of which are more translucent, and there is a tendency to an ochreous suffusion about the inner angle of the hind-wings. The beautiful red colour of this butterfly is variable and fleeting, and appears to fade even during the life of the insect. Very fresh specimens are usually of an exceptionally rich and brilliant coloration. *P. ridleyanus* bears a close resemblance to the red and black *Acraeas*, and especially to *egina*, with which it flies.¹ In the Congo State it has been taken with *Acraea rogersi*, the male of which somewhat resembles *A. egina* but is larger and has a greater extent of red in the hind-wings.

ACRAEA ORINA.

Hewitson, Ent. Mo. Mag., xi, p. 130 (1874).

— Exot. Butt., *Acraea*, pl. 7, ff. 43, 48 (1875).

— (♀ *oreta*), l. c., p. 131; l. c., f. 42.

Aurivillius (ab. *nigroapicalis*), Ent. Tidskr., xiv, p. 275 (1893).

Oberthür (ab. *orinata*), Étud. d'Ent., xvii, p. 22, pl. 2, f. 22 (1893).

Aurivillius, Rhop. Aeth., p. 113 (1898).

Plate VI, Fig. 11.

This common *Acraea* extends from Sierra Leone to Lake Victoria Nyanza, several examples having been taken at Entebbe, whence I have also received it. It varies in different examples in the extent of the red markings, and in some West African specimens the wings are almost transparent, and the red colour has a pale and faded appearance. The sexes are similar in appearance.

PSEUDACRAEA CLARKI.

Butler, Trans. Ent. Soc., p. 201, pl. 10, ff. 1, 1a (1892).

Aurivillius, Rhop. Aeth., p. 175 (1898).

Plate VI, Fig. 14.

At present this *Pseudacraea* is exceedingly rare. The single example in my own collection I received from Cameroon. It differs slightly from Butler's figure in the extent of the red markings. So far as is at present known it occurs only in West Africa, though in view of the wide range of the model, *Acraea orina*, we may not unreasonably expect it to have a wider distribution than has so far been disclosed.²

without significance. Meanwhile some interesting remarks by Mr. F. A. Heron on the subject of size in this connexion are recorded in the 'Proceedings of the Entomological Society' of 1903, pp. lxx, lxxi. After pointing out the probably defective sense of vision in regard to size, possessed by laterally-eyed insectivorous birds as compared with the frontal-eyed predatory birds, it was suggested that the size of a distasteful insect would impress an insectivorous bird less than would its colour and pattern, just as

a person might take immediate note of a poison label without paying much attention to its size.

¹ It is worth noting (as Mr. Trimen has pointed out to me) that Godart (l. c. p. 66) actually described a ♀ of this *Papilio* as a ♀ of his *Acraea zidora*. The type (the *Papilio*) is in the Edinburgh Museum.

² The *Charaxes acraeoides* of Druce (Ann. and Mag. Nat. Hist., Ser. 8, vol. ii, Nov. 1908) is described as somewhat resembling the above species. It is exceedingly rare, only one ♂ example being at present known.

CRENIS PECHUELI AND CRENIDOMIMAS CONCORDIA.

CRENIS PECHUELI.

Dewitz, Nov. Act. N. Cur. (41), ii, p. 195, pl. 26, f. 1 (1879).

— I. c. (50), p. 368, pl. 17, f. 2, ♀ (1887).

Aurivillius (*rosa* var.), Rhop. Aeth., p. 162 (1898).

Plate VI, Fig. 12, ♂.

Crenis pechueli may be distinguished from the closely allied *rosa* by the presence in the former on the fore-wing underside of a continuous submarginal row of black spots, whereas in *rosa* the spots do not extend beyond the space between the upper and lower radial. *C. rosa* is also of a somewhat richer mauve colour on the upperside. The two species overlap in Central Africa, but *rosa* is the eastern and *pechueli* the western species. The female of the latter has all the black markings more strongly marked. In the fore-wing the cell is suffused with black, and there is a rather indefinitely marked sub-apical black bar extending from the subcostal to about the middle of the hind-margin. In both wings there is a submarginal row of distinct round black spots.

In the cabinet the underside appears to be designed for conspicuousness. No doubt when the insect is in the open, and settled with closed wings it must be very conspicuous, but its usual habit is to settle high up on tree trunks, and Mr. Neave tells me that in this position it is very difficult to see. He found it common in North-West Rhodesia, where it was accompanied by *Crenidomimas concordia*.

CRENIDOMIMAS CONCORDIA.

Hopffer, Sitzb. Akad. Wiss., Berlin, p. 641 (1855).

— Peters, Reise Mossamb. Ins., p. 391, pl. 22, ff. 3, 4 (1862).

Butler (*Crenis crawshayi*), Proc. Zool. Soc., 1893, p. 654, pl. 60, f. 5 (1895).

Aurivillius, Rhop. Aeth., p. 205 (1898).

Plate VI, Fig. 15, ♂.

Mr. Neave tells me that this butterfly is exceedingly difficult to distinguish from *Crenis pechueli* when on the wing. The resemblance of the undersides is very remarkable. The complete orange-ochreous band of the hind-wing in *Crenis* is represented in *Crenidomimas* by a series of radiating sagittiform markings, which, combined with the discal band of black spots, produces a very similar effect. The habits and localities of *C. concordia* coincide in the west with those of *Crenis rosa*, and in the east with those of *C. pechueli*, whilst in the Upper Congo all three may be found together. The female has the black markings much more extended and suffused, giving the insect a very dark appearance, and corresponding with the same sex in *Crenis*.

P. VESTALIS AND P. STRIATA.

PLANEMA VESTALIS.

Felder, Reise Nov. Lep., p. 369, pl. 46, ff. 8, 9 (1865-7).

Hewitson (*curyta*), Exot. Butt. *Acraea*, pl. 4, f. 21 (1867).

Aurivillius, Rhop. Aeth., p. 122 (1898).

Plate VI, Fig. 13, ♂.

It is a somewhat difficult matter to separate the different forms of *Planema* into definite species. Many, especially West African forms, are very variable, and, whilst extreme forms are separable with but little trouble, there are many intermediate varieties the precise affinity of which is by no means clear. I have had the opportunity of examining some ten examples of *P. vestalis*, three of which are females, and in this species at least the pattern is fairly constant. The female is distinguished by its larger size and the more rounded outline of the

wings. As a rule the colours in this sex have a generally paler and more faded appearance, and the basal spots in the hind-wing are smaller, though in one example the basal spots are as distinct as in the male, and in one male the discal and basal reddish-ochreous is as pale as in the female. So far as I am aware the species is entirely confined to West Africa, in the region of Sierra Leone and the Gold Coast. Its only mimic, and that a very close one, is *Pseudacraea striata*.

PSEUDACRAEA STRIATA.

Butler, Cist. Ent., i, p. 215 (1874).

Hewitson (*Diadema eurytus*), *Diadema*, pl. 3, f. 9 (1868).

Aurivillius, Rhop. Aeth., p. 177 (1898).

Plate VI, Fig. 16.

A figure of this *Pseudacraea* appears on Plate III (*Diadema*) of Hewitson's beautiful series of figures of tropical butterflies, together with the male and female *Pseudacraea eurytus* and the female *Pseudacraea ruhamia*. All these forms were considered by the author to be varieties of one species, and it was their remarkable resemblance to species of *Planema* which caused him to break through his usual reserve and comment upon their similarity in a passage to which I have referred elsewhere (p. 105).

I have seen some twenty examples of this species. The specimen figured is in my own collection, and three others are in the Hope Department at Oxford, one being a female. The species is rather variable, my own example being a nearer approach to *vestalis* than the Oxford specimens, which are rather darker and somewhat devoid of the characteristic yellow suffusion of the *Planema*. The female is rather larger and paler than the male. The specimen figured was received from Sierra Leone.

THE PLANEMA EPAEA GROUP.

PLANEMA EPAEA.

Cramer, Pap. Exot., iii, p. 64, pl. 230, ff. B, C (1779).

Fabricius (*gea*), Spec. Ins., ii, p. 32 (1781).

Aurivillius, Synonymy, Rhop. Aeth., p. 119 (1898).

Plate VII, Fig. 1 ♂, 2 ♀.

Planema epaea is sexually dimorphic, the reddish areas in the male being replaced by white in the female. It is essentially a West African form, and it is probable that the males and females, as is frequently the case in dimorphic species, do not habitually fly together. I have examined a long series of both sexes and the markings appear to be extremely constant, the only difference being a slight variation in the richness of the colours, which may perhaps be due to variations in the age of the specimens when captured. The brown triangular mark at the base of the wing on the female underside is very characteristic of the *Planemas*, especially of the black and white forms, and is very faithfully reproduced in most of their mimics.

PSEUDACRAEA EURYTUS.

Linnaeus, Syst. Nat., ed. 10, p. 487 (1758).

Clerck, Icon. Ins. 2, pl. 31, f. 4 (1764).

Linnaeus (*euryta*), Mus. L. Ulr., p. 221 (1764).

Drury (♂ *hirce*), Ill. Exot. Ins., iii, p. 37, pl. 28, ff. 3, 4 (1782).

Westwood (♂ *gea*), in Drury, l. c., ed. 2, p. 38, pl. 28, ff. 3, 4 (1837).

Butler (♀ var. *epigea*), Cist. Ent., i, p. 216 (1874).

Aurivillius (♀ ab. *bicolor*), Rhop. Aeth., p. 176 (1898).

— Synonymy, Rhop. Aeth., p. 176 (1898).

Plate VII, Fig. 4 ♂, 5 ♀.

Pseudacraea eurytus exhibits a sexual dimorphism which exactly corresponds to that of its model *Pl. epaea*, and the mimicry is remarkably accurate on both surfaces. I have not had an opportunity of examining a long series of this species, but it does not appear to be liable to any important variation. The female variety *epigea* of Butler has the pale areas of the same reddish-yellow as is found in the male. Though that author described it as a new species, he suggested at the same time that it might only be a variety of the female *eurytus*, and this view Professor Aurivillius has adopted. The female form *bicolor* of the latter author has the fore-wings marked with white and the hind-wings with reddish-yellow. I have not seen any other example of this form, and it is probably a singular aberration. *Eurytus* occurs in the same localities as *Planema epaea*. The examples figured are from Sierra Leone.

PAPILIO CYNORTA.

Fabricius, Ent. Syst. (3), i, p. 37 (1793).

Westwood, Arc. Ent., i, p. 151, pl. 40, ff. 3, 4 (1843).

Boisduval (*zeryntius*), Spec. Gen. Lep., i, p. 370 (1836).

Westwood (♀ *boisduvallianus*), Arc. Ent., i, p. 151, pl. 40, ff. 1, 2 (1843).

Aurivillius, Rhop. Aeth., p. 469 (1898).

Neave (*peculiaris*), Novit. Zool., xi, p. 342 (1904).

Plate V, Fig. 17. Plate VII, Fig. 8.

This species is a member of the group which includes *P. echerioides*, *P. jacksoni*, and others in which, as has been indicated, many species are sexually dimorphic, and the females mimetic. The tails of the hind-wings are absent in both sexes. The male *P. cynorta* is black, with a pale cream-coloured band extending across both wings. In the fore-wing this band is very narrow near the apex, and becomes wider towards the inner-margin, and is separated into spots, wide apart at the apex but becoming more confluent towards the inner-margin. The spots are eight in number, the first being situated between the last two branches of the subcostal, and the second sometimes very small or obsolete. On the underside this band is chalky white, and the ground-colour umber-brown. There is a conspicuous golden-brown triangle at the base of the hind-wing, bearing two large black spots below the costal, three black streaks in the cell, and a black streak beneath the median and submedian respectively. The internervular rays are strongly marked in dark brown.

The typical appearance of the western female may be gathered from Plate VII, which also shows the close resemblance on both surfaces to *Planema epaea* ♀. This female was described and figured by the late Professor Westwood as *Papilio boisduvallianus* in his 'Arcana Entomologica', and it is remarkable that on the same plate he figures *P. cynorta*, the two forms not being then known to be the sexes of the same species. On June 5, 1878, Mr. D. G. Rutherford exhibited at the Entomological Society a specimen of a *Papilio* in which the left side of the wings showed the markings, more or less interrupted, of the male *cynorta*, whilst the right wings were those of *boisduvallianus*, thus confirming the relationship, the probability of which was pointed out by Trimen in 1868.

In some cases the female *P. cynorta* has a tawny suffusion in the hind-wings, this being especially the case in a specimen I have examined from Toro in West Uganda. It also varies somewhat in size, some examples being considerably larger than the figure on Plate VII. The species has a very wide range, as might be expected, since there is no lack of feasible models for the female form. On the west coast it occurs from Sierra Leone to Angola, and also extends eastwards to Toro in Uganda. The female undergoes a remarkable change as we proceed eastward, for although the typical western form occurs occasionally on the east side, as in the tawny specimen above referred to, the usual eastern form is the *peculiaris*

of Neave. That author, in the absence of fuller material, assigned *peculiaris* to *P. gallienus*, though it is now generally recognized as the eastern form of *P. cynorta*. I have figured this variety on Plate V, Fig. 17, together with its model, *Planema paragea*, Fig. 16, described and figured by Smith and Kirby (Rhop. Exot., 1901, p. 29, *Acraea*, Plate VII, Figs. 7, 8). *Planema paragea* is evidently closely allied to *epaea*. It is strange that the female *P. cynorta* should have developed in East Africa a pattern which, in the cabinet at least, appears to be much less conspicuous than that of the western form. It would seem as though *P. epaea*, in extending eastward, had undergone a modification to *paragea*, owing to causes which affected its own economy, and that in becoming modified it had carried the *Papilio* with it. I am indebted to the kindness of Mr. C. J. Grist for the opportunity of figuring the *peculiaris* form of *P. cynorta* from an example in his collection. The drawing of the *Planema* is from a specimen in my own collection. Both insects were taken at Entebbe.

PLANEMA AGANICE.

Hewitson, Exot. Butt., *Acraea*, pl. 1, f. 6 (1852).

Trimen, S. Af. Butt., i, p. 180 (1887).

Butler (var. *montana*), Proc. Zool. Soc., p. 91 (1888).

Rogenhofer (*montana* ♀), Ann. Mus. Wien., vi. p. 458, pl. 15, f. 2 (1891).

Vuillot (*bertha*), An. E. Fr. 60 Bull., p. 96 (1891).

Holland (*chanleri*), Proc. U. S. N. Mus., xviii, p. 748 (1893).

Aurivillius, Rhop. Aeth., p. 121 (1898).

Want of space has prevented me from figuring this *Planema*, though in view of the abundance of the species the omission will not, I trust, be a serious one. The male has an expanse of about $2\frac{3}{4}$ inches. The ground-colour of the fore-wings is nearly black. A pale narrow discal band, varying from creamy-white to ochre-yellow, beginning just beneath the costal nervure and divided by the nervules into eight somewhat elongate spots, the first five of which are continuous and parallel with the costa, the sixth and seventh broader, somewhat more distally placed, and directed towards the hind-margin, the eighth small and triangular, and lying between the first median and the submedian. The hind-wing has a broad curved discal band varying from creamy-white to ochre-yellow. A broad marginal band of brownish-black. The base of the wing dark red-brown with numerous black spots. On the underside the pattern is repeated but all the colours are paler, especially the brown triangular basal patch in the hind-wing, which is prominently spotted with black. At the base of the fore-wing, just above the origin of the costal nervure, is a small pale spot surrounded with black.

The female is often much larger. One example before me as I write has an expanse of $3\frac{3}{8}$ inches. The pattern is the same as in the male, but the discal bands are white, and often much broader and more continuous towards the inner-margin.

The variety *montana*¹ is more variable. The typical male resembles *aganice*, but the discal band in the fore-wings is broader and more continuous, and is deep orange-ochreous in colour. The dark marginal band in the hind-wing is narrower than in *aganice*, and the rest of the wing is dark orange-ochreous, the basal patch being usually only a little darker than the general colour.

¹ Trimen considers that *montana* is entitled to species rank (see Trans. Ent. Soc., 1908, p. 551, note), and though I have photographed the genitalia of *aganice* and *montana* and can find no appreciable difference between them, this particular evidence

taken alone is not sufficient. For the sake of uniformity I have retained the arrangement of Aurivillius, though at the same time I attach every importance to Mr. Trimen's opinion.

The female closely resembles that of *aganice*, but the white areas are of greater extent. One female I have examined has the discal area of the hind-wing pale ochreous, and one male has all the light areas of that colour.

The larva and pupa are thus described by Trimen (S. Af. Butt., i, p. 181):—

‘Larva. Pale whitish-green; the spines not rigid, very long, yellowish, set with inconspicuous black bristles. Head yellowish-brown, shining, the base slightly tridentate; mandibles black. Legs of the same colour as the body, longer than usual. Along middle of back, on segments four to eleven, a row of indigo-blue dots arranged in pairs between each subdorsal pair of spines; only one such spot on segments three to twelve. On each side, between subdorsal and lateral rows of spines, a row of larger indigo-blue spots, one on each segment from the second to the eleventh; spiracles ringed with the same colour; also an indigo-blue sub-spiracular festooned streak.

‘Pupa. Whitish-green. On back of abdomen four pairs of long divergent red spines, set rather widely apart; on each side between each spine and its successor two indigo-blue dots; on back of thorax three pairs of short tubercular processes, each marked with an indigo-blue dot; head with a pair of similar, longer, curved processes.’

The same author describes this butterfly as essentially a woodland species. It appears to be confined to the Natal region, and is represented in British and German East Africa by the variety *montana*, which has a much wider range, being common in the Belgian Congo (see note, Trans. Ent. Soc., 1908, p. 524). Marshall describes *P. aganice* (Trans. Ent. Soc., p. 413, 1902) as emitting a lot of acrid juice, ‘not only from the thorax, but also from the antennae and the nervules of the hind-wings.’

PSEUDACRAEA IMITATOR.

Trimen, Trans. Ent. Soc., p. 107 (1873).

— S. Af. Butt., i, p. 293, pl. 6, f. 1 ♀ (1887).

Aurivillius, Rhop. Aeth., p. 177 (1898).¹

Plate VII, Fig. 7, ♀.

Just as *Planema epaea* is represented in South Africa by *P. aganice*, so in the latter region we have *Pseudacraea imitator* taking the place of *P. eurytus*, to which it is closely allied. *P. aganice* presents no such wide difference between the sexes as does its West African representative, and so in correspondence we find the sexes of *P. imitator* are similar in appearance. It is still a comparatively rare species. I have only seen some half-dozen examples and have never received it in collections from abroad. Its close resemblance to *P. aganice* may have something to do with its rarity in collections. In describing the species, Trimen quotes from a letter he received from Colonel Bowker who forwarded him a pair from Pinetown. In this letter the writer says, ‘It is quite impossible to distinguish between this butterfly and *aganice*, either when settled or on the wing; and the first notice you get is the brittle *crunch* between finger and thumb of *imitator*, or the soft leathery feel of *aganice*. Death is, moreover, instantaneous with the former, while you may squeeze *aganice* as long and as hard as you like without effect; nothing but the poison bottle will settle him.’

I have been unable to find records of this species being taken in any region except Natal.

PSEUDACRAEA ROGERSI.

Trimen, Trans. Ent. Soc., p. 548 (1908).

Plate VII, Fig. 11, ♂; Fig. 14, ♀.

¹ Aurivillius includes *P. conradti*, Oberth., under this species; but *conradti* is evidently a very different form and has the paler markings brownish-yellow. It appears to resemble the ♂ *P. eurytus*.

This late addition to the species of *Pseudacraea* has only recently been described by the above author, and is represented at present by only one example of each sex. The male was taken about sixteen miles west of Shimba, near Mombasa, at an elevation of 1,200 feet, and the female at Rabai. The Rev. K. St. A. Rogers, who captured the female, states that in pattern and flight it was indistinguishable from *P. aganice*. The male was given to this collector, who forwarded it to Oxford, and remarked on its resemblance to the male *P. montana*. The female *Ps. rogersi* has a blue iridescence which is visible on the upper surface of the wings when viewed in certain lights. This structural colour is also observable in some specimens of the female of *Pseudacraea hobleyi*. *Ps. rogersi* is exceptionally interesting, completing, as it does, the series of these Pseudacraeinae mimics corresponding to the forms of the *Planema* models.

P. ELONGATA GROUP.

PLANEMA ELONGATA.

Butler, Cist. Ent., i, p. 212 (1874).

Aurivillius, Ent. Tidskr., xiv, p. 283 (1893).

Hewitson (*eurita*), Exot. Butt. *Acraea*, pl. 5. f. 28 (1867).

Aurivillius, Rhop. Aeth., p. 120 (1898).

Plate VII, Fig. 10, ♀.

This *Planema* was figured by Hewitson in 1867, who included the two sexes in the twelve figures which he considered to be various forms of what he then called *Acraea eurita*. Butler subsequently separated many of these forms into species, and to a pair of the present form in the National Collection he gave the name *elongata*. The sexes differ considerably. The male has much narrower fore-wings, rather darker in ground-colour, and with a tendency to concavity in the hind-margin. The lower extremity of the discal band is less inclined outwards towards the hinder angle than in the female, and is of a rich reddish-ochreous. In the hind-wing there is a triangular patch of dark reddish-brown, the dark hind-marginal border is narrower than in the female, and the discal area is rich reddish-ochreous with black nervules and internervular rays. Hewitson's examples apparently came from the Congo State. The pair in my own collection were received from Ogowe.

PSEUDACRAEA RUHAMA.

Hewitson, Ent. Mo. Mag., ix, p. 84 (1872).

— Exot. Butt (♀ *Diadema eurytus*), pl. 3, f. 8 (1868).

Butler (♀ *metaplanema*), Cist. Ent., i, p. 215 (1874).

Aurivillius, Rhop. Aeth., p. 177 (1898).

Plate VII, Fig. 13, ♀.

P. ruhama was figured by Hewitson in 1868 as one of the many forms of his *Diadema eurytus*, which he considered to be all varieties of the same species. In 1872 he described in the Ent. Mo. Mag. a male butterfly which he named *Diadema ruhama*, and which he received from Angola. This Professor Aurivillius considers to be of the same species as the form of *Diadema eurytus* above mentioned. Evidently the two sexes of the *Pseudacraea* mimic the corresponding sexes of *Planema elongata*. The species is extremely rare. There are two specimens in the Hope Department at Oxford which are both females, and are slightly different in appearance from the example figured, which is in my own collection, the fore-wing discal bar being less prominent and more suffused towards the hind-margin. In the National Collection there are five males and four females. The male is smaller than the female, has narrower wings, and the band in the fore-wings is narrower and reddish, instead of white as in the female.

PSEUDACRAEA GOTTBERGI.

Dewitz, Berlin. Ent. Zeit., xxviii, p. 187, pl. 1, f. 1 (1884).

Oberthür (*gazengeli*), Étud. d'Ent., xvii, p. 30, pl. 3, f. 31 (1893).

Aurivillius, Rhop. Aeth., p. 175 (1898).

I have been unable to obtain an example of this species to add to the illustrations. It was figured from a single male in the Berlin Ent. Zeit. in 1884, and is evidently a member of the *Planema elongata* association. The description given by Dewitz is as follows:—

‘Upperside. Fore-wings blackish-brown; a red-brown discal band extending from the subcostal to the inner-margin, and broken up by the black nervules. A deep black longitudinal streak in the cell, and dark internervular streaks. Hind-wings reddish-brown, blackish at base and margin, nervures and rays black.

‘Underside. Paler. Hind-wings with seven to eight round black basal spots in two rows.

‘Head and thorax with white, and abdomen with reddish-brown spots. Differs from *eurytus* and *ruhama* in the absence of black spots at base of fore-wing, and from *künowi* in the lack of the white band in the hind-wing.’

The male thus described mimics the male *Planema elongata*. I have not seen any description of the female, but it would be interesting to learn whether it is modified in the direction of the female *Planema*. The species occurs in Cameroon and the Congo region.

A. PHALANTHA AND P. HEGEMONE.**ATELLA PHALANTHA.**

Drury, Ill. Exot. Ins., i, p. 41, pl. 21, ff. 1, 2 (1773).

Cramer (*columbina*), Pap. Exot., iv, p. 92, pl. 337, ff. D, E (1782).

Herbst (♀ *phalanthus*), Naturs. Schmet., ix, p. 187, pl. 257, ff. 1, 2 (1798).

— (*laudonius*), l. c., p. 186, pl. 256, ff. 3, 4 (1798).

Trimen, Metamorph., S. Af. Butt., i, p. 191 (1887).

Aurivillius, Rhop. Aeth., p. 126 (1898).

Plate VII, Fig. 12 ♂.

This is one of the commonest butterflies in Africa and is found plentifully over the greater part of that continent, and also over a large portion of Tropical Asia. It is somewhat remarkable that so common and widely distributed a species has not more mimics in the African region.

PSEUDARGYNNIS HEGEMONE.

Godart, Enc. Meth. 9, p. 258 (1819).

Snellen (*duodecim punctata*), Tijds. v. Ent. (2), vii, p. 15, pl. 1, ff. 1-3 (1872).

Druce (*Aterica chlorana*), Trans. Ent. Soc., p. 157 (1874).

Aurivillius, Rhop. Aeth., p. 179 (1898).

Plate VII, Fig. 15.

This species has a very wide range extending from Cameroon to Mount Ruwenzori. It is probably not nearly so rare as was at one time supposed. Mr. Neave took a long series in the upper reaches of the Congo, and he informs me that it is quite indistinguishable from *A. phalantha* when on the wing, a fact which may be realized by a glance at the figures on Plate VII. The same collector once took an example amongst fourteen individuals of *A. phalantha*. The females often have darker spots, and the depth of the underside ground-colour varies in both sexes. In the dry season all the markings are frequently less distinct.

*THE PLANEMA POGGEI GROUP.***PLANEMA POGGEI.**

Dewitz, Nov. Act. Ac. Nat. Cur. (41), ii, No. 2, p. 18, pl. 1, f. 8 (1879).

Smith and Kirby (*♂ nelsoni*), Rhop. Exot., xix, *Acraea*, p. 10, pl. 3, ff. 9, 10 (1892).

Aurivillius, Rhop. Aeth., p. 120 (1898).

Plate VIII, Fig. 2, ♀.

This beautiful and characteristic *Planema* was first described by Dewitz, apparently from a female, as the male was subsequently described by Smith and Kirby as a distinct species under the name of *nelsoni*. The species was first reported from West Africa, Cameroon and Angola being given as localities. With the receipt of large collections from the neighbourhood of Entebbe we find, however, that, as with most species previously considered West African, it extends across to Lake Victoria Nyanza. At Entebbe it is very common. Judging by the number of its mimics, it may be regarded as an old-established and well-protected species. The female differs from the male in its larger size and much more rounded outline of wings. The most perfect mimics belong to the genus *Pseudacraea*.

PLANEMA MACARISTA.

E. M. Sharpe, Ann. Nat. Hist., vii, vol. xviii, p. 76 (1906).

Plate VII, Fig. 3 ♀. Plate VIII, Fig. 1, ♂.

This *Planema*, the male of which resembles *P. poggei* very closely, is distinguished by the narrowness of the yellow band in the fore-wing at the costa, by its serration on the lower distal side, and by the fact that the female is black and white. It occurs at Entebbe. There would appear to be several distinct species of *Planema* having males of the *poggei* coloration, the females being either like the male or black and white. The *Planema plagioscia* described by Bethune-Baker from a male in the Powell-Cotton collection (Ann. Nat. Hist., 8, vol. ii, p. 471, 1908) closely resembles *P. macarista*, but has the yellow bar deeply serrated on the apical distal outline. It was received from the Upper Congo. It is very remarkable that there should occur at Entebbe two species of orange-banded *Planemas*, the one having the sexes similar whilst the other has a black and white female, and in company with these we find *Pseudacraea künowi* with similar sexes, and also *Pseudacraea hobleiyi* in which the female is black and white like that of *Planema macarista*. The association of these forms is further complicated by the presence at Entebbe of *Planema alcinoe*, or an allied form very like *Pl. alcinoe*, var. *camerunica*, both sexes of which are described and figured by Professor Aurivillius (Ent. Tidskr., xiv, p. 285, Plate 6, Figs. 4, 5, 1893). The male is a tawny and brown form resembling some of the West African *Planemas*, whilst the female is a large black and white insect very similar to the female of *Planema macarista*, but usually to be distinguished by the much browner colour of the hind-wing basal area.

The affinities of the forms of *Planema alcinoe* are not yet very clearly defined, and the resemblance at Entebbe between the females of this species and those of *P. macarista* has caused some difficulty. The two examples mentioned by Neave in Novit. Zool., xi, p. 348, 1904, and identified as *Planema godmani* are females of *Planema macarista*. *Planema godmani* appears to be the female of *Pl. alcinoe*, whilst the female described by Butler as *salvini* is labelled in the National Collection as identical with the female *camerunica*. So far as can at present be discerned we must therefore tabulate the forms as follows:—

Planema alcinoe, Felder.

Felder, Reise Novara. Lep., p. 368, pl. 46, ff. 12, 13 ♂ (1865-7) (Sierra Leone).

= *godmani*, Butler, An. N. H. (6), xvi, p. 415 ♀ (1895) (Sierra Leone).

var. *camerunica*.

Aurivillius, Ent. Tidskr., xiv, p. 285, pl. 6, ff. 4, 5, ♂ and ♀ (1893) (Cameroon).

= *salvini*, Butler, An. N. H. (6), xvi, p. 415, ♀ (1895) (Cameroon).

PSEUDACRAEA KÜNOWI.

Dewitz, Nov. Act. Ac. Nat. Cur. (42), ii, p. 198, pl. 2, f. 6 (1879).

Aurivillius, Rhop. Aeth., p. 175 (1898).

Plate VIII, Figs. 5, 7.

This rare species was originally described by Dewitz from a single male specimen taken in the western upper reaches of the Congo. It is a very perfect mimic in both sexes of *Planema poggei*, and like *Ps. hobleiyi* it apparently occurs more commonly near Entebbe, where *P. poggei* is especially abundant, in fact all the specimens I have seen are from that region. It still remains extremely rare. As a species it is very distinct, there being no nearly allied form at present known.¹ It is remarkable that whereas *P. hobleiyi* is sexually dimorphic and mimics the two sexes of *P. macarista*, *P. künowi* is similar in both sexes.

PSEUDACRAEA HOBLEYI.

Neave, Novit. Zool., xi, p. 331 (1904).

— (*tirikensis*), l. c., p. 332 (1904).

Plate VII, Fig. 6, ♀. Plate VIII, Fig. 8.

This *Pseudacraea*, the male of which bears so close a resemblance to *Planema poggei* and *P. macarista*, also bears in that sex a great similarity to the preceding species of its own genus. It may be recognized, however, at once, without examination of minute details, by the fact that there are *two* black internervular rays between the submedian and the first median in the hind-wing instead of one as in *P. künowi*. It may also be distinguished by the prominent black spots in the basal area of the hind-wing, and in the cell of the fore-wing, and by its generally rather less expanse of wing. As in *P. künowi* the mimicry extends to the under-side. *P. hobleiyi* is a rather variable species, some examples of the male having the orange bar extending to the hind-wings, and the richness of this colour also varies considerably in different specimens. It may be noted that the extension of the orange to the hind-wings also occurs occasionally in the model, and frequently in *Acraea alciope* ♀ *aurivillii*. *P. hobleiyi* presents a very interesting case of sexual dimorphism. The female was first described from three examples, two of which were at first thought to be males, and the species was named *tirikensis*. A further examination, however, assisted by the acquisition of more material, showed that the form *tirikensis* was always female, and further that *hobleiyi* was always male. As the two forms always occur together, there can be little doubt that they are the sexes of one species for which the name *hobleiyi*, originally given to the male form, must stand. A careful examination of the extensive material at the Tring Museum has further convinced me that *hobleiyi* and *tirikensis* are the sexes of the same species, and also that they are the eastern representatives of the western *Pseudacraea simulator*, Butler, the male of which is very like that of *P. hobleiyi*, but has the hind-wings tawny, the black spots more prominent, and the fore-wing band less distinct. The female *P. simulator* is not unlike the female *P. hobleiyi* (*tirikensis*), but has a brownish-white basal area in the hind-wings, upon which the usual black spots are more prominent than upon the dark basal area of *hobleiyi*. The sexes of *P. simulator* mimic those of *Planema excisa*, Butler, or an allied form. The female *P. hobleiyi* is, as will be seen from the figure, a very perfect mimic of the female of a large black and white female of *Planema macarista* (Plate VII, Fig. 3). The sexes of many butterflies have quite different habits, and thus we may account in the first place for the resemblance between the dimorphic sexes of *P. simulator* and those of *Planema excisa*. As we proceed eastwards to Uganda, *P. simulator* is represented by *P. hobleiyi*, the sexes of which find suitable models in the dimorphic *Planema macarista*. *Pseudacraea hobleiyi* has so far only been received from the neighbourhood of Entebbe, where it occurs not uncommonly in company with its two models.

¹ Since the above was written I incline to the belief that *Ps. gottbergi* is closely allied to this species.

PRECIS RAUANA.

Grose Smith (*Junonia*), Novit. Zool., v, p. 352 (1898).

Aurivillius (var. ? *milonia*), Rhop. Aeth., p. 139 (1898).

Plate VIII, Fig. 11.

In the absence of a figure, Professor Aurivillius has placed this species under *Precis milonia* as a probable variety. The genus *Precis* exhibits to a greater degree than any other African butterflies the phenomenon known as seasonal dimorphism. Much light has been thrown on our knowledge of this subject by the extensive and valuable experiments made by G. A. K. Marshall, an account of which was given by Professor Poulton in their joint paper in Trans. Ent. Soc., 1902.¹ The above experimenter succeeded in breeding *Precis sesamus* from *Precis natalensis* and the startling nature of this result may be gathered from the fact that whilst *P. natalensis* is a salmon-red butterfly, *P. sesamus* is dark blue. Another species, *P. simia*, was also shown to be the wet-season phase of *P. antilope*. Not only are the seasonal forms of *P. sesamus* very different in appearance, but they also differ considerably in habits. The wet-season or summer form *natalensis* frequents open spaces, whilst the *sesamus* form prefers shady places, is very wary, and when alarmed flies off rapidly, and settles suddenly, when its cryptic underside causes it to disappear. The very peculiar development in this species of cryptic coloration in the dry phase and a conspicuous appearance in the summer form, is the subject of a very interesting discussion by Professor Poulton in a part of the paper referred to. It is to be noted that winter forms of tropical butterflies very frequently exhibit a cryptic modification, especially of the underside.

Generally the species of the genus *Precis* do not exhibit strong mimetic tendencies, and the female of *P. rauana* is exceptional in showing so marked a development in the direction of the model *Planema poggei*. The male is slightly smaller and is without the white suffusion on the hind-wings.

The remaining members of this group are the *planemoides* variety of the female *P. dardanus*, a form of *Elymnias phegea*, the eastern female of *Acraea alciope*, and the peculiar *semifulvescens* form of *Acraea johnstoni*, each of which is described under a special section dealing with the polymorphic forms of the respective species. The *Planema poggei* group forms an exceedingly interesting illustration of the influence of a dominant type on the surrounding forms which, through their instability and capacity for variation, have been enabled to develop patterns which produce such close resemblances. Moreover, the coincidence in geographical distribution of the group is exceedingly perfect. In West Africa we find *P. poggei* accompanied by *Ps. künowi*, *Acraea alciope aurivillii* ♀ (two examples only recorded), and probably by the corresponding form of *Elymnias phegea*. The first example of the *planemoides* form of *P. dardanus* known to exist in collections was taken in 1873 in Angola, showing that that protean butterfly had there come under the influence of the model, but all these forms were rare until *P. poggei* was discovered in larger numbers at Entebbe. There we find it accompanied by all its former mimics, but with the interesting addition of *Pseudacraea hobleiyi* and the female *Precis rauana*, together with the permanent establishment of the eastern female of *A. alciope*. These facts are much too remarkable to partake of the nature of coincidences, and demand some better explanation than those of similarity of environment and local conditions, so commonly advanced by the opponents of the mimetic theory.

¹ Five Years' Observation and Experiments on the Bionomics of S. African Insects, Marshall and Poulton, Trans. Ent. Soc., 1902. Marshall's original paper appeared in Ann. and Mag. Nat. Hist. (7), vol. ii, 1898.

*THE PLANEMA TELLUS GROUP.***PLANEMA TELLUS.**

Aurivillius, Ent. Tidskr., xiv, p. 280, f. 7 (1893).

Staudinger (*epitellus*), Iris, ix, p. 207 (1896).

Aurivillius, Rhop. Aeth., p. 119 (1898).

Plate VIII, Fig. 3.

This conspicuous *Planema* was originally described from Cameroon, though it extends to Uganda, and I have received it commonly from Entebbe. The female is somewhat larger than the male, and has the fore-wings especially much more rounded, whilst some examples have a tendency to a whitish suffusion in the sub-apical bar in the fore-wings. Many West African specimens have the sub-apical bar smaller than in those from the east, and the markings of the fore-wing are often more irregular.

PSEUDACRAEA TERRA.

Neave, Novit. Zool., xi, p. 332 (1904).

Plate VIII, Fig. 6.

This form of *Pseudacraea* was first observed in the large collection received from Entebbe, and described by Neave in the paper above referred to. It was then represented by one male example. It is still a rare insect, and is invariably taken in company with *Planema tellus*, which it so closely resembles. As the *Planema* is a very common insect it may be that *P. terra* is not in reality so rare as it at present appears, though I have lately had an opportunity of examining a collection which included a very large number of specimens of the *Planema*, and even in this there are comparatively few examples of the mimic. The sexes do not appreciably differ in appearance, but there is a tendency to vary somewhat towards a whitish suffusion similar to that observed in the model. All the specimens with which I am acquainted were taken at Entebbe.

MIMACRAEA DARWINIA.

Butler, Lepid. Exot., p. 104, pl. 38, f. 8 (1872).

var. *apicalis*.

Smith and Kirby, Rhop. Exot., xiii, p. 41, pl. 10, ff. 6, 7 (1890).

Aurivillius, Rhop. Aeth., p. 266 (1898).

Plate VIII, Fig. 17 (*apicalis*).

This Lycaenid I have received together with *Planema tellus* from Cameroon, and there can be little doubt that it presents an approximation towards the *Planema* pattern. It does not appear to be so rare as the other members of its genus, though it has not, so far as is at present known, extended its range across Africa to the Victoria Nyanza, and we have very little information as to its habits and natural surroundings. Judging from the fact that the type form *darwinia* is only represented by one specimen and that the variety *apicalis* is not uncommon, it would appear that the latter is in reality the usual form and that *darwinia* is the variety. The latter differs from *apicalis* in having the sub-apical mark in the fore-wing of the same shade as the ground-colour of the wings.

ACRAEA JODUTTA.

Fabricius, Ent. Syst. (3), Part I, p. 175 (1793).

Dewitz (*♂ flava*), Nov. Act. Acad. Nat. Cur. (41), ii, No. 2, p. 19, pl. 1, f. 10 (1879).

Möschler (*gea*), Abh. Senck. Ges., xv, p. 55 (1887).

Doubleday and Hewitson (*♀ carmentis*), Gen. D. Lep., p. 140, pl. 19, f. 1 (1848).

Aurivillius, Rhop. Aeth., p. 116 (1898).

Plate VIII, Fig. 9, ♀.

This exceedingly variable *Acraea* has a very wide range extending from Sierra Leone to Uganda. The majority of the males from the neighbourhood of Entebbe resemble Fig. 9 in the arrangement of the markings, but the light areas are of a pale ochreous colour, and in the female these markings are white. In one female the sub-apical bar is white, whilst the inner-marginal patch and discal portion of the hind-wing are ochreous and much reduced in area. A female from Sierra Leone has the dark hind-wing border reddish-brown, and the nervules and rays black. The black and white female is that figured by Doubleday and Hewitson under the name of *carmentis*. This form undoubtedly mimics the black and white *Planemas*, and is synposematic with *P. epaea*, *P. alcinoe*, &c. The most interesting variety of the female is that illustrated on Plate VIII. Here the sub-apical bar, the inner-marginal patch, and the greater part of the hind-wings have all developed the tawny orange of *Planema tellus*. This peculiar form has been taken at Entebbe by Dr. Wiggins in company with its model and also with the peculiar form of *A. encedon* previously described (p. 36). It is not, however, confined to the east, as there exists in the Hope Museum at Oxford an example of the same variety with the tawny areas somewhat richer in colour, which was taken in West Africa. This example is not easily distinguishable from the male *Planema epaea*. It seems appropriate here to note the remarkable parallel between the varieties of *A. jodutta* and *Acraea esebria*. Each variety of *A. jodutta* is represented by a corresponding form of *A. esebria* and without the opportunity of comparing long series it is not always an easy matter to assign individual examples to their respective species. A comparison between large numbers of specimens shows that in *A. esebria* the sub-apical bar of the fore-wing is smaller, more clearly defined, and more distinctly divided by the nervules, whilst the marginal border of the hind-wings is narrower and very clearly defined. *A. esebria* is essentially a South African insect, though some of the varieties are found in Angola.

ACRAEA ALTHOFFI.

Dewitz, Ent. Nachr., xv, p. 102, pl. 1, f. 5 (1889).

Aurivillius (*rubrofasciata*), Ent. Tidskr., xvi, p. 111 (1895).

— Rhop. Aeth., p. 107, 1898.

Smith and Kirby, Rhop. Exot., *Acraea*, pl. 8, ff. 3, 4 (1901).

Plate VIII, Fig. 12, ♀ var.

This *Acraea* has at least three varieties of female. The form nearest to the male in pattern has been described to me by Mr. H. H. Druce. The male is slightly larger than Fig. 12. The ground-colour is brownish-black. The fore-wing has a sub-apical bar of a brick-red colour, rather nearer to the end of the cell than to the apex, and consisting of one large spot beginning below the subcostal, and divided by the nervules, and a small separate spot slightly dusted with pale yellow, and placed between the second and third median nervules. A red streak occupying the lower half of the cell, very narrow at the base, and widening suddenly beyond the middle so as to reach the subcostal; and a red discal band extending from the second median to the inner-margin, and deeply indented on the basal side above the first median. The hind-wings with a narrow discal curved band of pale yellow, extending from the costa a little beyond the middle to the middle of the inner-margin. Dark internervular rays on the marginal border, bifurcate distally, and enclosing elongate paler spots. A few small black spots on the dark basal patch. On the underside the fore-wing is pale red with a sinuous discal band of dark brown. The sub-apical bar much paler than on the upperside, and the apical and hind-marginal areas dark ochreous with black internervular rays bifurcated on the margin and enclosing pale spots. Two black spots in the cell, the first small, the second elongated, transverse, and extending from the subcostal to the median. A black spot above and a little beyond the origin of the

first median nervule, and two spots below the first median, the inner one much the smaller. Hind-wing discal band paler than on the upperside, hind-marginal border dark ochreous with dark brown internervular rays, bifurcate, and enclosing white spots. Basal patch reddish-ochreous with numerous black spots. Head, thorax, and abdomen brown above and paler below. Abdomen ringed and spotted with orange.

Mr. Druce describes his specimen of the female as being very much like the male, but slightly paler. The sub-apical band is yellow, but the upper portion of it is dusted with red scales. The discal band of the hind-wing is considerably broader than in the male. The example was taken at Entebbe. The female described by Smith and Kirby is very like that figured on Plate VIII, but the ground-colour is nearly white. I have lately seen several examples of this variety, which appears to be an approach towards the black and white *Planemas*. The ochreous form of the female which I have figured is commoner than the others, at least in localities where *Planema tellus* is abundant.

Few better instances could be found of the influence of a dominant model on the surrounding species than these varieties of other butterflies which are so obviously being modified in the direction of *Planema tellus*. The right-hand column of figures on Plate VIII forms a most striking illustration of the phenomenon. *Pseudacraea terra* has already arrived at so close a resemblance to the model that it is quite indistinguishable from it when on the wing. In *A. jodutta*, *A. althoffi*, and the variety of *A. encedon* we can see very distinctly the tendency of these species to assume the orange-tawny colour of the *Planema*, and the case of that very adaptive species *A. encedon* should be specially observed in view of the criticism, duly considered in a later portion of this volume, that there is no evidence that the butterflies which now resemble one another were ever dissimilar.

A. OBERTHÜRI AND M. NEAVEI.

ACRAEA OBERTHÜRI.

Butler, An. Nat. Hist. (6), xvi, p. 271 (1895).

Staudinger (*bonasia*), Exot. Schmet., i, p. 84 (1885) (non Fabr.).

Oberthür (*cynthius*),¹ Étud. d'Ent., xvii, p. 27, pl. 1, f. 5 (1893).

Aurivillius, Rhop. Aeth., p. 107 (1898).

Plate VIII, Fig. 14, ♂.

Acraea oberthüri is a West African insect, and occurs in the Cameroon region, and in Angola and Gaboon. I have only had an opportunity of examining a comparatively small number of examples, judging from which it does not appear to be a variable species. The female is larger than the male, and has all the colours somewhat paler.

MIMACRAEA NEAVEI.

Eltringham, Ent. Mo. Mag., Aug., p. 172 (1909).

Plate VIII, Fig. 15.

So far as I am aware, the specimen figured is the only example yet received. As will be seen, the resemblance to *A. oberthüri* is so close that it might well be passed over if mixed with a large number of the latter species. A little paler in colour than the specimen of *A. oberthüri* figured, the mimicry is nevertheless extremely close. My specimen is not quite perfect, and presents the appearance of being slightly worn, so that in life the butterfly is probably still more like the model. The species was taken in Cameroon, where *oberthüri* is very plentiful, and as with other comparatively rare mimics it has doubtless hitherto been frequently overlooked. I am inclined to regard the example as a female, though owing to the absence of the forefeet, it is difficult to determine the sex with certainty.

¹ Oberthür's figure certainly represents *A. oberthüri*. The identity of Drury's '*cynthius*' is very doubtful. Butler regards it as an albino form of the *bonasia* of Fabricius.

MIMICRY IN THE *PIERINAE*

It might be supposed that, in view of the conspicuous appearance of the *Pierinae*, mimicry produced by close resemblances in detailed markings would be to some extent overshadowed by the predominating feature of white wings. Nevertheless there is considerable evidence that the detailed characteristics of what in Africa appears to be the dominant genus, viz. *Mylothris*, are faithfully copied by species of several other genera, notably by forms of *Phrissura*, which constitute mimetic pairs with many species of the former genus. The forms of *Mylothris* are themselves extremely difficult to differentiate into species, and pending further investigation I have followed the specific names given by Professor Aurivillius in his 'Rhopalocera Aethiopica', wherein are enumerated some twenty-eight species. The exceedingly accurate mimicry which obtains between species of different genera of African *Pieridae* has been productive of considerable confusion of nomenclature. To deal adequately with the subject of Pierine mimicry would involve a careful revision of the species and genera, and an exhaustive study of many varieties, all of which would be inappropriate to the scope of the present work. In spite of a sense of incompleteness I must content myself, therefore, with calling attention to the Pierine forms certainly belonging to different genera which exhibit apparently mimetic patterns. Any lack of unanimity at present existing as to the use of certain specific names does not materially affect the aim of the work.

MYLOTHRIS AGATHINA.

Cramer, Pap. Exot., iii, p. 76, pl. 237, ff. D, E (1779).

Trimen, S. Af. Butt., iii, p. 30 (1889).

— Metamorph. S. Af. Butt., iii, p. 31, pl. 2, f. 3 (1889).

Aurivillius, Rhop. Aeth., p. 394 (1898).

Plate IX, Fig. 1, ♂, Fig. 9, ♀.

The female *M. agathina* varies from the appearance shown on Plate IX to a rich orange colour, the vermilion flush at the base of the fore-wing being more or less accentuated. The species has a wide range, apparently occurring over the whole of Tropical Africa. The larva and pupa are thus described by Trimen :—

'Larva. Transversely barred with alternate dull red and blackish bands speckled with yellow; and clothed generally with fine grey hair of some length; a yellowish-white lower lateral stripe on each side, from second to last segment immediately above the legs. Head black, varied with yellow down the middle. Length, $\frac{3}{4}$ inch.

'Pupa. White, more or less tinged with cream-colour in parts, and curiously marked with black. Head with a long frontal horn, curved upward, cream-coloured. Thorax cream-coloured dorsally, but with a broad black marking along the middle; a small anterior acute black tubercle on each side, and on median ridge a series of three white, black-edged, broad, blunt, tubercular processes, slanting forward. Wing-covers black with a greenish tinge. Abdomen dorsally white and black, the latter forming a large lozenge-shaped marking (widest on seventh segment) acuminate anteriorly on fifth and posteriorly on ninth segment; on each side a row of small black spots; below these a broad black stripe; along median ridge a series of seven small white black-edged tubercles, of which the second, third, and fourth are blunter and larger than the rest; both the sixth and seventh segments bearing on each side a large, broad, acute, slightly forward curved, tooth-like white projection; anal extremity very pointed. Length $\frac{2}{3}$ inch. Attached by anal extremity and thoracic silken girth to web of silk spread on a leaf.'

Speaking of the butterfly the same author records that it is 'rather a heavy flyer, haunting wooded spots, and is very conspicuous on the wing'.

The top row of figures on Plate IX show the undersides of five butterflies of different genera, the first being the present species. The similarity of pattern in these insects is very remarkable. The species are as follows :—

PHRISSURA PHOEBE.

Butler, Proc. Zool. Soc., p. 936, pl. lviii, f. 67 (1900).

Plate IX, Fig. 2, ♀; Fig. 20, ♀.

The butterfly figured as above corresponds as nearly as possible with the *phoebe* of Butler, though it might perhaps also be referred to *isokani*, Grose Smith. I have examined Butler's figure, and the specimen shown at Fig. 2 differs only in the absence of a slight orange suffusion along the hind-margin of the hind-wing. Fig. 20 on the same plate differs only from Butler's figure in the fact that the latter has yellowish hind-wings. The example at Fig. 2 was taken on the north-east shore of Lake Victoria Nyanza, and that at Fig. 20 was recorded from Sierra Leone. The male is white with a pinkish flush at the base of the fore-wings, and a powdery black border, narrow along the costa, broad round the apex, somewhat broken up towards the hind-angle, and blacker and indentate on the nervules. The hind-wing has a marginal border of large, rounded, powdery black spots on the nervules. The underside is white with minute black dots at the ends of all the nervules.

PINACOPTERYX RUBROBASALIS.

Lanz, Iris, ix, p. 116 (1896).

Aurivillius (*Pieris*), Rhop. Aeth., p. 412 (1898).

Plate IX, Fig. 3, ♀.

Occurs in British East Africa. On the upperside the female is rather dull white, with a powdery black border on the fore-wings, and a black spot between the second and third median. A slight pink flush at the base. Hind-wings with an orange mark at base above the subcostal, and a yellow suffusion round the anal angle. A small black dot at end of each nervule. The male is pure white on the upperside and is without the discal spot.

BELENOIS THYSA.¹

Hopffer, Monats. Akad. Wiss. Berlin, p. 639 (1855).

— Peters Reise, Mos. Ins., p. 349, pl. 21, ff. 7–10 (1862).

Trimen (*agathina* var.), Rhop. Af. Aust., p. 29 (1862).

— (*thysa*), S. Af. Butt., iii, p. 44 (1889).

Butler (*sabrata*), Trans. Ent. Soc., p. 526 (1870).

— (var. *meldolae*), Proc. Zool. Soc., p. 725 (1871).

Aurivillius, Synonymy, Rhop. Aeth., p. 409 (1898).

Plate IX, Fig. 4, ♂; Fig. 10, ♀.

This species occurs from Angola to East Africa. The example figured is from Mombasa. On the upperside, as in the other species here described, the male resembles the male *M. agathina*, being white with marginal black spots. The female resembles that of *M. agathina* on both surfaces, the uppersides being shown together at Figs. 9 and 10.

¹ Professor Aurivillius gives this species under the name *larima*, Boisd., but I have for the present purpose retained the name *thysa* as that attached to the specimen figured, and which is in the Hope

Department at Oxford. The same author also puts *Pinacopteryx* and *Belenois* in one genus, *Pieris*. But they are now separated in the British Museum.

ERONIA ARGIA.

Fabricius, Ent. Syst., p. 470 (1775).

Herbst, Naturs. Schmet., v, p. 78, pl. 90, f. 1 (1792).

Cramer (♂ *cassiopea*), Pap. Exot., iii, p. 14, pl. 201, f. A (1782).

Aurivillius (var. ♀ *semiflava*), Ent. Tidskr., xvi, p. 262 (1895).

Boisduval (var. ♀ *idotea*), Sp. Gen. Lep., i, p. 441 (1836).

Donovan (var. ♀ *poppea*), Nat. Repos., ii, pl. 54, f. 2 (1824).

Aurivillius (var. ♀ *mixta*), Ent. Tidskr., xvi, p. 262 (1895).

— (var. ♀ *sulphurea*), l. c.

Trimen (var. *varia*), Trans. Ent. Soc., p. 175 (1864).

Aurivillius, Synonymy, Rhop. Aeth., p. 446 (1898).

Plate IX, Fig. 5, ♀.

This common butterfly extends from Sierra Leone to Natal. The male varies from white to pale greenish-blue, and has a black hind-margin in the fore-wing, broad at the costa and narrowing to a point near the inner-margin. There is no red flush at the base of the wings. On the underside the fore-wings are the same as on the upperside, but paler, yellowish about the costa and hind-margin, and the hind-wings are very pale ochreous, with a slight dusting of blackish scales near the margin and below the second subcostal. A very minute black dot at the extremity of each nervure except the costal and submedian. The females are usually whitish above, with a suffused and broken brown marginal border in both wings. This border varies from nearly black to a mere powdering of the nervules. On the underside the peculiar purplish-brown stain-like markings on the margin of the wings also vary greatly in intensity. It seems probable that the underside markings are a combination of cryptic and aposematic coloration. In the position of partial repose the orange flush at the base of the fore-wings would be visible and synaposematic with that of *Mylothris agathina*. In complete repose this aposeme would be concealed and the insect would undoubtedly bear a very close resemblance to a dead leaf. The latter fact will be completely realized by any one who has examined the very beautiful plate in Trans. Ent. Soc., 1907, showing *Eronia cleodora* on the wing and at rest. In the latter position the markings of the hind-wing, which are not unlike those of *E. argia*, so perfectly represent the decayed leaves of *Isoglossa woodii* that the insect becomes practically invisible, in much the same way as do the species of the genus *Kallima* referred to in the introductory section.

MYLOTHRIS SPICA.

Möschler, Verh. z. b. Ges. Wien., xxxiii, p. 277 (1883).

Boisduval (♀ *eudoxia*), Spec. Gen. Lep., i, p. 510 (1836).

Möschler (♂ *poppea*, var. c.), l. c., p. 275 (1883).

Karsch (♂ *jaopura*), Berlin Ent. Zeit., xxxviii, p. 232 (1893).

Aurivillius, Metamorph. Ent. Tidskr., xvi, p. 258, pl. 2, f. 2 (1895).

— Synonymy, Rhop. Aeth., p. 393 (1898).

Plate IX, Fig. 6, ♀; Fig. 14, ♂.

It is extremely difficult to distinguish between this species and the *Mylothris poppea* of Cramer (Plate IX, Fig. 15, ♀), and it is doubtful whether they are specifically distinct, though the female *M. poppea* is usually white, as shown in Fig. 15, instead of having the fore-wings yellow. I have illustrated this white female *M. poppea* in order to show the close resemblance between it and the female *Phrissura phoebe*, depicted at Fig. 20. The male *M. poppea* is similar to the male *M. spica*. As will be seen from the figures, the appearance of the two sexes is very different. The female *M. spica* shown at Fig. 6, was taken in Southern Nigeria, whilst I received the male from Sierra Leone. The pupa is thus described by Professor Aurivillius (loc. cit.):—

‘The pupa from which a male emerged must have been white or greenish, and differs

in important points from that of *agathina* figured by Trimen. The spine on the head is quite straight, sloping upwards and black anteriorly. Close behind this spine, at the margin of the anterior part of the thorax, are two small processes. The thorax is carinate and angulated in the middle. The first segment of the abdomen is very small, carinate, and with a small process on each side. The remaining segments are very broad and flattened dorsally. The second and third have on each side two long, blunt, finger-like processes, and the fourth only one such projection. The second and fourth of these processes are black. Segments four to eight are distinctly carinate.'

PHRISSURA SYLVIA.

Fabricius, Ent. Syst., p. 470 (1775).

Möschler (♂ and ♀ var. *rhodope*), Verh. z. b. Ges. Wien., xxxiii, p. 273 (1883).

Aurivillius (*Appias*), Rhop. Aeth., p. 398 (1898).

Plate IX, Fig. 7, ♀; Fig. 19, ♂.

The two sexes of *P. sylvia* are almost indistinguishable from those of *M. spica*. In fact, as with most of these resemblances between species of the two genera, they can scarcely be separated, except by the generic characteristics. The male specimen figured was received from Sierra Leone, and the female is from Lagos.

ERONIA THALASSINA.

Boisduval, Spec. Gen. Lep., i, p. 443 (1836).

Ward (♂ *verulanus*), Af. Lep., p. 4, pl. 4, f. 5 (1873).

— (♀ ab. *verulanus*), l. c., ff. 6, 7.

Aurivillius, Synonymy, Rhop. Aeth., p. 447 (1898).

Plate IX, Fig. 8, ♀.

This butterfly is common all over Tropical Africa. The male is very different in appearance from the female, and is a pale blue insect with a black margin in the fore-wing, very narrow along the costa, broad at the apex, and becoming narrower again towards the hind-angle. The female varies from white to cream colour, the fore-wings being suffused with dull yellow. I have examined Ward's figure of the female (*verulanus*), and it differs but little from my figure on Plate IX, and principally in the presence of two sub-apical yellow spots on the dark apical border of the fore-wing; the fore-wings are also of a richer yellow colour. Ward's figure of the male is coloured rather a vivid green, but the colouring is probably somewhat exaggerated. The female bears a very perfect resemblance to that of *M. spica*. The male is an exceedingly beautiful insect, especially on the underside, which in the hind-wings has a delicate greenish-silvery appearance.

MYLOTHRIS ASPHODELUS.

Butler, Proc. Zool. Soc., 1887, p. 572 (1888).

Dewitz (*poppea*), Nov. Act. Ac. N. Cur., xli, 2, pl. 25, f. 11 (1879).

Snellen (*phileris*), Tijdschr. v. Ent., xxv, p. 227 (1882).

Aurivillius, Synonymy, Rhop. Aeth., p. 393 (1898).

Plate IX, Fig. 11, ♂.

This form is distinguished from *M. spica* by the pale yellow suffusion at the base of the fore-wing. Aurivillius (Ent. Tidskrift, 1895, p. 259) describes the female as very similar to that of *M. spica*, but with a more yellowish ground-colour in the fore-wing, and a shorter and broader marginal band. The example figured is from the Congo State.

PHRISSURA PERLUCENS.

Butler, Trans. Ent. Soc., p. 431 (1908).

Plate IX, Fig. 16, ♂.

This species, the male of which closely resembles that of *M. asphodelus* was found by Butler in the Hewitson collection, and described by him as above. The female is described by the same author as resembling that sex of *P. sylvia* in pattern, but having the ground-colour of all the wings on the upperside pure white. The examples described were from Angola and the Gold Coast. The male figured on Plate IX was taken at the same time and place as the specimen of *M. asphodelus*.

MYLOTHRIS TRIMENIA.

Butler, Cist. Ent., i, p. 13 (1869).

Staudinger, Exot. Schmet., p. 29, pl. 17 (1884).

Trimen, S. Af. Butt., iii, p. 33 (1889).

Trimen (*agathina* var.) Rhop. Af. Aust., p. 29, pl. 2, f. 2 (1862).

Aurivillius, Synonymy, Rhop. Aeth., p. 395 (1898).

Plate IX, Fig. 12, ♂; Fig. 13, ♀.

Unlike so many of the species of this genus, *M. trimenia* appears to be tolerably distinct, and not to graduate by variations into other forms. It always has the fore-wings white, and in the male lemon-yellow, and in the female ochre-yellow hind-wings. Trimen remarks in his work above quoted that when on the wing it much resembles faded yellow leaves drifting before the breeze, and that Mr. J. P. Mansel Weale had independently recorded the same impression. The species occurs in Cape Colony and as far north as Abyssinia. Both the examples figured were captured by Dr. Longstaff in Queen's Park, East London.

PHRISSURA LASTI.

Smith, An. Nat. Hist. (6), iii, p. 124 (1889).

Smith and Kirby (*Belenois*), Rhop. Exot., xxii, p. 5, pl. 2, ff. 1-3 (1892).

Aurivillius (*Appias*), Rhop. Aeth., p. 399 (1898).

Plate IX, Fig. 17, ♂; Fig. 18, ♀.

There is but little to remark in regard to this species of *Phrissura* beyond the fact that it resembles very closely in both male and female the corresponding sexes of *M. trimenia*. The examples figured were taken in British East Africa, by Mr. Rogers, at Rabai.

The figures and instances here given by no means exhaust the known examples of Pierine mimicry in the African region. Nearly every form or species of *Mylothris* is accompanied by a species of *Phrissura* which closely resembles it in one or both sexes, and there are frequently forms from the other genera represented by the first row of figures on Plate IX, which are members of the groups thus centred round species of *Mylothris*. Dr. Dixey, in 1907, at the meeting of the Entomological Society, on Nov. 20, exhibited no less than sixteen groups of this nature, representing the same number of definite patterns, presented in all but two instances by a species of *Mylothris*. The mimics included thirteen *Phrissura*, nine *Pinacopteryx*, twelve *Belenois*, and eleven *Eronia*. The mimicry exhibited by these Pierine forms is probably, in some genera at least, Müllerian in nature. *Mylothris* is certainly comparatively distasteful. An experiment is described in a later portion of this volume in which a baboon seized a *Mylothris agathina* and a *Belenois mesentina*, putting them both in its mouth at once. It then put them out, picked up the *Mylothris* again and refused it a second time, then seized the *Belenois* and ate it. Another baboon then picked up the discarded *Mylothris*, but after tasting it at once rejected it. This interesting experiment, whilst not

necessarily showing that the *Belenois* was particularly palatable, certainly shows that it was less distasteful than the *Mylothris*, and thus whilst other Pierine butterflies may be more or less distasteful, it may well be that it is an additional advantage to resemble a species of the latter genus. It is interesting also to note that besides the aposematic patterns of the uppersides and the basal red or yellow warning mark of the undersides, all of which are displayed when the insect is more or less on the alert, it is evidently an advantage to many of these insects to avoid being attacked when in complete repose, and the portion of their pattern then displayed is in many cases purely cryptic. This is notably the case in many species of *Eronia*, which in the attitude of complete rest and therefore the state of minimum alertness, become practically invisible, although when the fore-wings are not completely hidden within the secondaries the red flush at the base of the former will act as an aposeme. I am inclined to think that such species as present an extremely cryptic appearance in repose are in all probability more Batesian than Müllerian mimics, and in this class I should be inclined to place the members of the genus *Eronia*. In Africa its species have not developed mimetic patterns to anything like the extent that obtains in the Oriental region. There many or most of the species, more particularly in the female sex, have developed mimicry of Danaine butterflies to a degree which can only be compared with the Pierine mimicry of the *Heliconidae* in the Neotropical region. With regard to the combination of cryptic and aposematic coloration, instances are by no means wanting in other orders of insects; and it is well known that many grasshoppers (*Acridiidae*), extremely cryptic under ordinary circumstances, exhibit, when alarmed, the often brilliant colours of their wings, previously concealed beneath the tegmina. Such colours are not necessarily a sign of actual distastefulness. The sudden appearance of brilliant colours may, and probably often does, have the effect of startling an enemy and so frightening it away, quite apart from any suggestion of distastefulness.¹

FURTHER INSTANCES OF MIMICRY IN THE *LYCAENIDAE*

It has already been remarked that mimicry in the *Lycaenidae* is a common phenomenon in the African region, and it now remains to describe some further mimetic *Lycaenidae* in addition to the forms of *Mimacraea* and *Pseudaletis* already noted. Several species of *Mimacraea*, of which lack of space has prevented my giving illustrations, are more or less mimetic of *Acraeas* and *Planemas*. Thus *M. charmian*, Smith and Kirby, which somewhat resembles the male of *M. fulvaria*, but has a larger expanse of reddish-orange on both wings, presents a general Planemoid appearance. *M. krausi*, Dew., is not unlike *M. poultoni*, to which it is probably allied, and mimics the western representative of *A. sotikensis*, viz. *A. praeponina*, Staud. *M. neokoton*, Druce, resembles on the upperside *M. marshalli*, though the orange areas are paler, the sub-apical band yellow, and the species has a generally Acraeine appearance. The *Mimacraea neurata* of Holland I have not seen. The following are instances of mimicry in other genera :—

PENTILA AMENAIDA.

Hewitson, Exot. Butt., *Pentila and Liptena*, pl. 2, ff. 4-7 (1873).

Aurivillius (var. *nyassana*), Rhop. Aeth., p. 261 (1898).

Plate IX, Fig. 26.

¹ Mr. Trimen informs me that he has noticed that several species of the larger *Saturniidae* in South Africa, resting with the hind-wings for the most part covered by the fore-wings, when disturbed or

molested would suddenly display, and *keep displayed*, the usually brightly coloured hind-wings, with their great conspicuous central ocellus like a vertebrate eye.

This butterfly extends from the Congo State to British East Africa. It is indistinguishable on the wing from *Pardopsis punctatissima*, which ranges from the Cape to Abyssinia. I have selected *P. amenaida* as perhaps the best mimic of *P. punctatissima*, though many other species of the genus are similarly marked, notably *Pentila clarensis*, Neave, which is difficult to distinguish on the upper surface from *P. amenaida*, but has a characteristic marginal row of elongated black spots on the underside of both wings. It is found at Entebbe. The southern *Pentila tropicalis*, Boisd., has very few spots, a paler ground-colour, and usually a dark apical border, and resembles a *Terias*. The western *Pentila abraxas* is white with black apices and a few black spots, and a reddish suffusion at the base of the wings, and resembles a small Pierine. *Pentila amenaida* is accompanied at Taveta by a Geometrid moth, *Petovia dichroaria*. Mr. Rogers describes them as very similar when on the wing. Marshall describes the same moth as flying with and resembling *Alaena amazoula* in Natal. The genus *Pardopsis*, of which the species *punctatissima* forms the model of *P. amenaida*, is one of the three African genera of *Acraeinae*, and is represented by this single species. The genus was founded by Trimen, who describes the species as having a low and weak flight, and frequenting wooded spots.¹ In the present state of our knowledge of the distribution of the species the *Pentila* would seem to have a wider range than the *Pardopsis*, and if this be the case it would point to the mimicry being of a Müllerian character. In connexion with these insects Rogers states (Trans. Ent. Soc., p. 534, 1908) that the Lycaenid gives the impression of being itself protected. 'It is very fond of settling in little companies on low plants, and if disturbed often opens its wings a few times without quitting the surface on which it is resting. Its flight is very feeble indeed.' From this description there can be but little doubt that the species is distasteful.

CITRINOPHILA SIMILIS.

Kirby, An. Nat. Hist. (5), xix, p. 366 (1887).

Smith and Kirby, Rhop. Exot., iii, *Lycaen. Af.*, p. 11, pl. 3, ff. 1, 2 (1888).

Kirby (*♂ marginalis*), An. N. H. (5), xix, p. 368 (1887).

Smith and Kirby, Rhop. Exot. E., p. 13, pl. 3, ff. 5, 6 (1888).

Aurivillius, Rhop. Aeth., p. 269 (1898).

Plate IX, Fig. 27.

There is very little in the appearance of this butterfly to suggest its Lycaenid affinity. The male was described by Kirby as *C. marginalis*, and the female as *Teriomima similis*. The male has more black, especially on the fore-wing, where it projects along the discocellular nervules. The only example I have seen is the female figured on Plate IX, which was taken near Benin, in Southern Nigeria. It is a wonderful mimic of the common and ubiquitous *Terias brigitta*, Cramer, an example of which from the same region is shown at Fig. 22.

TERIOMIMA XANTHA.

Grose Smith, Rhop. Exot. *Lycaen. Af.*, p. 140, ff. 13, 14 (1901).

Plate IX, Fig. 25.

Though the colour of this Lycaenid is not quite so bright a yellow as in species of *Terias*, it nevertheless presents a very close mimicry of the latter type of coloration, approximating especially to that of *Terias senegalensis*, Boisd.,² shown at Fig. 23. Several other forms

¹ For observations on the distastefulness of this species see p. 115.

² In naming this species I have followed the plan adopted by Butler in his revision of *Terias* (Ann. Mag. Nat. Hist., 1898, vol. i, pp. 66, 67), where the name

floricola is restricted to examples from Madagascar, though the specimen figured might, so far as appearance goes, be termed *floricola*. I am indebted both to Mr. Trimen and to Dr. Dixey for assistance on this point.

of *Teriomima* resemble species of *Terias*, though the colour of the former is generally a more tawny yellow.

LIPTENA HOMEYERI.

Dewitz, Berlin. Ent. Zeit., xxviii, p. 188, pl. 1, ff. 3, 3a (1884).

Aurivillius, Rhop. Aeth., p. 278 (1898).

Plate IX, Fig. 28.

When viewed in the cabinet this butterfly does not appear to be a very obvious mimic of *Terias*, and it is in such cases that the evidence of a naturalist who has seen the insects in their habitual surroundings is of great value and interest. Mr. Neave, who took a long series of *L. homeyeri* in North-East Rhodesia, informs me that it is most difficult to distinguish the difference in the shade of yellow when the insects are flying together. The species appear to be common, and, as in many of these instances, the mimicry is probably Müllerian.

LARINOPODA TERA.

Hewitson, Ent. Mo. Mag., x, p. 125 (1873).

Dewitz (*soyauxii*), Nov. Acta Ac. N. Cur. (41) ii, p. 201, pl. 26, f. 10 (1879).

Aurivillius, Rhop. Aeth., p. 273 (1898).

Plate IX, Fig. 29.

There are several white *Lycaenidae* which closely resemble small Pierines. *L. tera* presents a very good example of this form of Lycaenid mimics. The specimen figured was taken at Entebbe, where its model *Leptosia medusa* (Plate IX, Fig. 24) is also found. Other white species of the genus are *L. lircea*, Hew., which resembles *L. tera*, but the apex of the fore-wing is blacker, *L. aspidos*, Druce, which is smaller and has a rather broad black apex, and *L. brenda*, Druce, which is only distinguishable from *L. aspidos* by the black spots in the hind-wing.

CITRINOPHILA ERASTUS.

Hewitson, Exot. Butt., *Pieris*, pl. 8, f. 51 (1866).

— *Pentila* and *Liptena*, p. 2, text (1873).

Kirby (♂ *erasmus*), An. Nat. Hist. (5), xix, p. 366 (1887).

— (♀ *flaveola*), l. c.

Smith and Kirby, Rhop. Exot., *Lycean. Af.*, p. 19, pl. 5, ff. 1, 2, 3, 4, 5 (1888).

Aurivillius, Rhop. Aeth., p. 269 (1898).

Plate IX, Fig. 30, ♀.

In 1866 Hewitson figured a Pierine butterfly from the Gaboon River which he named *bernice*, and which is now known as *Mylothris bernice*. It is creamy-white with a flush of deep yellow at the base of the fore-wing costa. There is a narrow black line along the costa widening towards the apex and continuing round the hind-margin, where it breaks into spots. There are six black spots on the margin of the hind-wing, and the whole insect is not unlike *M. asphodelus* figured on Plate IX, Fig. 11, but the yellow flush is confined to the costa. Immediately above this figure is an illustration of *Citrinophila erastus*, which he describes as *Pieris erastus*. No better testimony to the essentially Pierine appearance of this Lycaenid could be found than the error of this famous butterfly artist. Hewitson, as is well known, was bitterly opposed to the mimetic theory, and it must have been extremely trying to have to subsequently acknowledge '*Pieris*' *erastus* as a Lycaenid, which he did seven years later, assigning it without comment to his genus *Liptena*.¹ I have described *M. bernice* above at some length as it is this Pierine which *erastus* closely resembles. *C. erastus* appears to be

¹ It is of interest to note that the error was pointed out to Hewitson by Trimen in 1867.

rare, and I have seen but few examples. The male is somewhat yellower, and has a broader black border continued in the hind-wing. The species occurs in the Gaboon country.

EPITOLA HONORIUS.

Fabricius, Syst. Ent. (3), i, p. 151 (1793).

Hewitson, Ill. D. Lep., p. 17, pl. 1a, ff. 3-5 (1878).

Aurivillius, Rhop. Aeth., p. 291 (1898).

The Acraeine appearance of the underside of this beautiful Lycaenid is almost startling. The male is about $2\frac{1}{2}$ inches in expanse and has the fore-wings black with a glittering blue suffusion extending from the base along the cell and from the median nearly to the margin. There is a line of blue along the anterior side of the costal, bending obliquely across the wing from a point midway between the end of the cell and the apex, and reaching the lower radial. The space between this and the end of the cell is occupied by a dull area forming what appears to be a sexual brand. The hind-wings are almost entirely black, but dusted with blue, broadly on the costa and inner-margin, and narrowly on the hind-margin. On the underside the fore-wing is sepia-brown basally. There is a line of indistinct white spots crossing obliquely from half-way between the end of the cell and the apex, to the inner angle. Apex dull ochreous. A slight dusting of metallic blue on the discal area. Orange-ochreous at base above the costal. Hind-wing brownish-ochreous with very indistinct discal narrow white bar, beginning about middle of costa and bent suddenly outwards at the second median, along which it runs to the margin. Base suffused with deep orange-ochreous, and having eleven small but well defined black spots. The hind-margin of the fore-wing is concave, giving the apex a slightly hooked appearance. The female is quite different on the upper-side. The fore-wing is well rounded. The ground-colour is dark sepia-brown, and there is a broad white oblique discal band reaching to the hind-angle. Below the median is a metallic blue streak. The hind-wing is rather paler brown with a white central patch suffused with blue basally and towards the inner-margin. The underside resembles that of the male, except that the white band in the fore-wing is reproduced.

It is remarkable that this butterfly should have developed such perfect Acraeine mimicry on the underside, retaining on the upperside the usual Lycaenid appearance. I have only seen one other instance of a similar modification, viz. in *Hewitsonia boisduvali*, Hew., where the hind-wing underside is somewhat similarly marked, though the ground-colour is much paler.

PAPILIO DARDANUS AND SUBSPECIES.

PAPILIO HUMBLLOTI.

Oberthür, Ann. Ent. Soc. France (6), 8 Bull., p. 40 (1888).

— Étud. d'Ent., xiii, p. 9, pl. 1, ff. 1, 2 (1890).

Aurivillius, Rhop. Aeth., p. 466 (1898).

PAPILIO MERIONES.

Felder, Reise Nov., Lep., p. 95 (1865).

Trimen, Trans. Linn. Soc., xxvi, pl. 42, f. 1 (1869).

Boisduval (*brutus*), Faune. Mad., p. 12 (1833).

Aurivillius, Rhop. Aeth., p. 466 (1898).

PAPILIO ANTINORII.

Oberthür, Ann. Mus. Genov., xviii, p. 711, pl. 9, f. 4 (1883).

Kheil (var. ♀ *niavioides*), Iris, iii, p. 335, f. 1 (1890).

— (var. ♀ *ruspinae*), Iris, iii, p. 335, f. 2 (1890).

Aurivillius, Rhop. Aeth., p. 464 (1898).

Rothschild and Jordan (*dardanus antinorii*), Novit. Zool., xii, p. 187 (1905).

PAPILIO DARDANUS.

- Brown, Ill. Zool., p. 52, pl. 22 (1776).
 Cramer (*merope* ♂), Pap. Exot., ii, p. 87, pl. 151, ff. A, B (1777), and pl. 378, ff. D, E (1781).
 Fabricius (*brutus* ♂), Spec. Ins., ii, p. 13 (1781).
 Palis. Beauvois (*sulfurea* ♂), Ins. Af. et Amer., p. 46, pl. 1 (1805).
 Fabricius (*hippocoon* ♀), Ent. Syst. (3), i, p. 38 (1793).
 Cramer (*niavius* ♀), Pap. Exot., iii, p. 71, pl. 234, f. A (1779).

- Boisduval (*westermanni*), Spec. Gen. Lep. i., p. 372 (1836).
 Doubld. and Hew. (*dionysos* ♀) Gen. D. Lep., p. 20, pl. 3, f. 4 (1846).
 Aurivillius (ab. *nioboides* ♀), Hew. Exot. Butt. Pap., pl. 12, f. 39 (1869).
 Aurivillius (ab. *niobe* ♀), Hew., l. c., f. 40.
 — Rhop. Aeth., p. 464 (1898).
 Trimen (var. *planemoides* ♀), Proc. Ent. Soc., p. 40 (1903).
 Rothschild and Jordan (*dardanus dardanus*), Novit. Zool., xii, p. 187 (1905).

PAPILIO CENEA.

- Stoll, Suppl. Cram., p. 134, pl. 29, ff. 1, 1a (1791).
 Godart (*brutus* ♂), Enc. Meth., ix, p. 69 (1819).
 — (*rechila* ♀), Enc. Meth., ix, p. 183 (1819).
 Trimen (*merope* ♂), Rhop. Afr. Austr., p. 11 (1862).
 — (*merope* ♂ and ♀), Trans. Linn. Soc., xxvi, p. 508, pl. 43, ff. 1, 3, 4 (1869).
 — (*cenea* ♂ and ♀), Trans. Ent. Soc., p. 169, pl. 9, ff. 1, 2 (1881).
 Haase (*hippocoonides* ♀), Bib. Zool. (8), i, p. 70, pl. 2, f. 8 (1891).

- Westwood (*trophonius* ♀), An. Nat. Hist., ix, p. 38 (1842).
 — Arcana Ent., i., p. 153, pl. 39, f. 1, 2 (1845).
 Aurivillius, Rhop. Aeth., p. 465 (1898).
 Rothschild and Jordan (*dardanus cenea*), Novit. Zool., xii, p. 187 (1905).
 Trimen (*dorippoides* ♀), Trans. Ent. Soc., p. 554 (1908).
 Poulton (*trimeni* ♀), Trans. Ent. Soc., p. 283 (1906).

PAPILIO DARDANUS POLYTROPHUS.

- Rothschild and Jordan, Novit. Zool., x, p. 488 (1903).

- Poulton (*trimeni* ♀), Trans. Ent. Soc., p. 283 (1906).

PAPILIO DARDANUS TIBULLUS.

- Kirby (*tibullus* ♂), Proc. R. Dub. Soc. (2), ii, p. 338 (1880).

- Rothschild and Jordan, Novit. Zool., xii, p. 187 (1905).

Plate X, Figs. 1-15.

The case of *Papilio dardanus* and its various races and subspecies presents by far the most extraordinary instance of butterfly mimicry as yet known, not only in Africa but throughout the world. The earliest reference to the species is that of Brown in 1776 as given above. The male was figured by Cramer in 1777, but was shown without tails to the hind-wings, an error due no doubt to his having access to only one example, and that a damaged one.¹ The species presents an astonishing instance of female polymorphism, and a glance at the principal references given above shows how numerous are the forms under which it has been described. In 1779 Cramer figured a black and white butterfly which he called *niavius*, and in 1791 Stoll figured in his supplement to Cramer's great work the butterfly which was described as *Papilia cenea*. It was not until many years later that the true relations obtaining between these butterflies were even suggested, and the story of the gradual solution of the mystery is one of the romances of natural history. At this stage the reader will do well to examine Plate X, on which the principal varieties of this butterfly are figured, and reference to the illustrations will be of material assistance in following the descriptions.

As has already been described, the publication of Bates's paper on mimicry in South American butterflies caused naturalists in other parts of the world to investigate the phenomenon in those regions with which they were familiar. Wallace contributed a valuable

¹ In his subsequent figure (pl. 378, D, E) Cramer gave the tails.

paper dealing with mimetic forms in the Oriental region, whilst Trimen laid the foundation of our knowledge of the subject as illustrated by the butterflies of Africa, and it is to the distinguished African naturalist that we owe the original discovery of the relationship of the forms of *Papilio dardanus*, the first account of which was given in Trimen's paper in the Transactions of the Linnaean Society in 1869. The males were found commonly in the woods about Knysna, on the south coast of Cape Colony in 1858, but it was some time before the *cenea* form was observed, and the first example captured was taken for *Amauris echeria*, and the author tells us how, being then unaware of the extent to which sexual dimorphism existed, he was at first inclined to regard the butterfly he had captured as a hybrid between *merope* and *echeria*. Subsequently other examples of the *cenea* form were taken, and also two of the *trophonius* form, which, needless to say, did not tend to elucidate the mystery. In 1866 Trimen had read Bates's paper, and Mrs. Barber forwarded specimens of *cenea* from Grahamstown, with a request for a male of that species, from which to make a drawing. No such thing, however, as a male *cenea* could be found, and independently of this fact it was observed that all the available examples of *Papilio merope* were males. In 1867 Trimen came to England and there found that in all the accessible specimens *merope* was of the male sex, whilst *cenea*, *trophonius*, *dionysos*, and *hippocoön* were invariably females, and with the boldness which frequently characterizes great discoveries, he stated, in his paper already referred to, his opinion that these diverse tailless forms were all females of the one long-tailed black and white *Papilio merope*. It was hardly to be expected that this view would be immediately accepted, and the most strenuous opponent of the theory, for it was then still unproved, was W. C. Hewitson, who published his opinion very emphatically in the text which accompanied his plate illustrating forms of *dionysos* and *hippocoön*. These forms he recognized as varieties of the same species, but, whilst recognizing them as females, he declined to believe that they were the females of *merope*, and thus expresses his views:¹ 'That the butterflies now figured are all females there cannot, I think, be a doubt; but that they are the females of *P. merope*, as suggested by Mr. Trimen, I do not for one moment believe. *P. merope* of Madagascar, has a female the exact image of itself; and it would require a stretch of the imagination of which I am incapable to believe that the *P. merope* of the mainland, having no specific difference, indulges in a whole harem of females differing as widely from it as any other species in the genus. . . . It is true that we have of late been introduced to some strange anomalies in the sexes, but to none which bear comparison to this. In the orange-banded *Epicalias* there is no resemblance certainly between the male and female, either in colour or the arrangement of the spots, but there is no total disagreement in form. In the two species of *Papilio* which have lately been united, *torquatus* and *caudius*, and *argenteus* and *torquatinus*, though much unlike each other, there is quite sufficient resemblance not to shock one's notions of propriety. Mr. Trimen, in the paper of the Transactions of the Linnaean Society, in which he discusses this subject, and details the biography of *P. merope* from its first creation in Madagascar to its subsequent wonderful polymorphisms on the Continent, says that "entomologists, no less than naturalists generally, appeared content with a child-like wonder at this and kindred facts, and let them pass as things inscrutable" until Mr. Darwin gave us a "rational explanation of these phenomena". I must say, and I hope I may do so without giving offence to any one, that I prefer the child-like attitude of former naturalists to the childish guesses of those of the Darwinian school.' It is interesting in this connexion to note that in 1874 Hewitson received from Fernando Po *P. merope* and *P. hippocoön* taken in coitu, which he

¹ Hewitson, Exotic Butterflies (1869).

thus records in the Entomologist's Monthly Magazine (vol. ii, p. 113): 'Mr. Rogers has sent me a second collection of butterflies from Fernando Po, containing *Papilio merope* and *P. hippocoön* taken by him in copulation, another illustration of the saying that "truth is stranger than fiction". I find it very difficult (even with this evidence) to believe that a butterfly, which, when a resident in Madagascar, has a female the image of itself, should, in West Africa, have one without any resemblance to it at all.'

The first proof of the specific identity of *cenea*, *hippocoön*, *trophonius*, and the black and white male, was obtained by Mr. Mansel Weale, who found a number of the larvae near King William's Town. From these larvae were bred seven males, four females of the *cenea* form, one of the *trophonius*, and one of the *hippocoön*. These results were communicated to the Entomological Society in 1874, and we can imagine with what triumphant satisfaction the announcement must have been received by the naturalist whose intelligent anticipation had been received with such scepticism. In recent years further experiments have confirmed these results. In September, 1902, Mr. G. F. Leigh, of Durban, succeeded in taking a pair of *cenea*, the female being of the white-spotted *cenea* form.¹ From this female ninety eggs were obtained, of which only three proved sterile. After going through various transformations which will be described later, and a few larvae being preserved, ultimately fifty-six pupae were obtained, eleven of which failed to emerge successfully. Forty-five specimens were thus obtained, of which twenty-seven were females and eighteen males. The males were of the normal form, whilst three of the females were of the southern *hippocoön* form, and the remainder *cenea*. Three of the *cenea* forms had buff spots on the fore-wings corresponding to *Amauris echeria*, whilst the remainder were white-spotted resembling *albi-maculata*. From this brood no examples of *trophonius* were obtained. Many of the specimens were examined by Professor Poulton,² who found that there was a gradual gradation from the white-spotted to the buff-spotted forms, and also that the black marginal band in the male hind-wing exhibited great variation. In 1903 the same experimenter was fortunate enough to capture a female of the *trophonius* form, from which seven eggs were obtained, which ultimately produced five butterflies. Of these, three were males and two females, the latter being of the white-spotted *cenea* form. It is noticeable that the *trophonius* eggs did not produce any imagines of that form, though the number of ova obtained was too small to draw any definite conclusion therefrom. The next experiments in breeding *P. dardanus* were carried out in 1904 by the same naturalist, and the results described by Professor Poulton in Trans. Ent. Soc., 1906.³ Eggs were collected from a *trophonius* female near Durban, and six males and seven females were obtained from the larvae. Of these females six were of the *cenea* form and one typically *trophonius*; the *cenea* form showed the same variations from white to buff spots as were observed in the former brood. The males had the submarginal band in the hind-wings distinctly less heavily marked. Leigh's further experiments have resulted in three more families of *dardanus* being bred from ova, one in 1906 and two in 1907. A very complete and interesting discussion on all these families was communicated to the Entomological Society in 1908 by Professor Poulton.⁴ In the 1906 family there were fourteen males, and the same number of females, of which latter eight were of the *cenea* form, three *hippocoön*, and three *trophonius*, the female parent being of the *hippocoön* variety. The first of the 1907 families arose from ova of the *cenea*

¹ For a full account of these breeding experiments see Synepigonic series of *Papilio cenea*, Trans. Ent. Soc., p. 667, 1904, G. F. Leigh.

² l. c., p. 680.

³ Poulton, Mimetic Forms of *P. dardanus* (*merope*), Trans. Ent. Soc., p. 281, 1906.

⁴ Poulton, Heredity in Six Families of *P. dardanus*, Trans. Ent. Soc., p. 427, 1908.

form, which produced fifteen males and seventeen females, one of which was *hippocoön* and the rest *cenea*. The last family arose from a *hippocoön* female, and contained seventeen males and thirteen females, all the latter being of the *cenea* type. Perhaps the most obvious point elucidated by these breeding experiments is the fact that the males do not appear in anything like the overwhelming proportion in which they are observed in nature; in fact, excluding the case in which only five specimens were reared, in only one instance did the number of males even exceed that of the females, and then only in the ratio of seventeen to thirteen, whilst the total sum of individuals shows eighty females to seventy-three males, thus showing that the scarcity of females in the field is apparent rather than real. The next point to strike the observer is the great preponderance of *cenea* and the rarity of *trophonius*. We should expect the *cenea* form to be plentiful in view of the predominance of *Amauris echeria*. On the other hand, *chrysippus* is also plentiful, and we should expect the corresponding form *trophonius* to be at least as common as the others. Such, however, is not the case and the *trophonius* form is everywhere rare. This fact has been remarked upon by Trimen (Trans. Ent. Soc., 1904, p. 688), and the subject has been still more fully dealt with by Professor Poulton (l. c.). In discussing the predominance of the forms of *dardanus*, that author points out that, judging from a large collection received from the Chirinda Forest in South-Eastern Rhodesia, the predominating form appears to be *hippocoön*, which was found in the proportion of twenty-two to one of *cenea* and one of *trophonius*. In spite of this fact, *Amauris dominicanus* is by no means the predominant model in the district in question; indeed, judging from the numbers actually collected, *Amauris lobengula*¹ and *albimaculata* greatly outnumbered the black and white *Amauris*, as did also *D. chrysippus*. The conclusion arrived at is, that bearing in mind that *A. dominicanus* is nevertheless a common butterfly at Chirinda, whereas in Natal it is rare, it may be that the black and white *Amauris* confers a greater benefit on the mimic by its greater conspicuousness, especially in the forest. The question of the relative efficiency of the different Danaine models is, however, a subject which requires considerable further study. Dealing with the rarity of *trophonius*, the author points out that whilst *dardanus* is a forest insect, *D. chrysippus* frequents more open regions, and thus the influence of the latter as a model would be to a great extent limited to those areas where forest and open country were contiguous. Hitherto we have been considering three forms of the female *dardanus*, but these by no means complete the list of known forms of this protean butterfly. The form *dionysos* described by Doubleday and Hewitson in 1846 is, so far as we know at present, confined to the west coast. As will be seen from a reference to the plate, it resembles the *hippocoön* form, but has the ground-colour of the hind-wings yellow. It is decidedly rare in collections and can only be regarded as either a primitive intermediate form or a reversion occurring sporadically. Figs. 4 and 8 represent two extremely interesting varieties, *niavioides* and *ruspinae*, of the Abyssinian subspecies *antinorii* taken at Lake Tana by the late Dr. Stecker. These two butterflies are at present absolutely unique, no other examples ever having been received. I am indebted to the publishers of Haase's work on mimicry for permission to copy their figures of the insects which I understand are now at Prague. They were described and figured by Kheil in 1890. As will be seen, *niavioides* presents the *hippocoön* form, but retaining the tails of the hind-wings, whilst *ruspinae* is distinguished by having the whole of the basal area in both wings reddish-yellow, as in the *trophonius* variety of the other subspecies. These butterflies remain something of a mystery. They may be an ancestral form of *hippocoön* and *trophonius*, and may have occurred by reversion.

¹ A form nearly resembling *Amauris echeria*.

But in the absence of fuller data and further specimens, we can hardly argue anything of prime importance from these two isolated examples. In his Presidential address to the Entomological Society in 1898 Trimen described a form of female *cenea* from Zanzibar which was much less modified from the male than even the form *dionysos*, and which appeared to be a reversion to the original colour of the female. Some years later several examples of this variety were received from Kikuyu Escarpment, and the form was described by Professor Poulton,¹ who gave it the name of *trimeni*. It is one of the females of the subspecies *dardanus polytrophus* (R. and J.). The example I have figured on Plate X is now in the Hope Department at Oxford. It will be noted that the ground-colour is less modified from that of the male than in any of the other varieties, whilst the somewhat indeterminate nature of the darker markings on the fore-wing exhibits a perfect transition between the general appearance of the males of the group and that of the *hippocoön* form. This transition is very beautifully shown in the series of examples of *polytrophus* in the museum referred to. The specimen figured is nearest to the male in colour and pattern. In the next specimen the dark areas are much blacker and more definitely outlined, whilst in a third example the pale sub-apical bar and the broad black hind-wing margin are still more clearly marked. In a specimen of the *hippocoön* variety of this subspecies the principal change is that of the ground-colour which is now white, and the darker areas are brownish rather than black. From this point we get, on the one hand, the definite *hippocoön* form by the blackening and stronger definition of all the dark areas, and, on the other hand, the *cenea* form by the separation of the sub-apical bar into spots and the extension of the black area along the inner-margin of the fore-wing. Fig. 15 shows a specimen intermediate between Fig. 3 and the *cenea* variety, the latter being very simply produced by the whitening of the spots in the fore-wing and the darkening of the yellow of the hind-wing basal area. There are also in this series two extremely interesting intermediate specimens, one being like the advanced form of *trimeni*, but with the whole of the ground-colour reddish-yellow, like *trophonius*, whilst the other has paler reddish basal areas in both wings and the spots of the ancestral pale buff colour. It will be noted that the example of *trimeni* figured on Plate X shows the rudiment of a tail in the hind-wing in the same way as does the specimen of *hippocoön* at Fig. 5.

The next female variety is that described by Trimen,² and named *planemoides*. The example exhibited at the meeting of the Entomological Society in October of 1903 was taken in Uganda, and the only other then known specimen was taken in 1873 in Angola. This form is a wonderful mimic of *Planema poggei* (Dewitz), an insect which acts as a model for so many butterflies in the neighbourhood of Entebbe. A specimen is figured on Plate X, Fig. 12. The resemblance of the *Papilio* to the *Planema* had already been recognized by Neave, who worked out the larger collection in which it was included. *Planemoides* presents a somewhat striking departure from the other varieties, as will be seen from the figure. It is interesting and important to observe that this form only occurs in the same regions as the *Planema* which it imitates, the variety not having been found to occur in the other subspecies of *dardanus*. The form has not hitherto been bred from the ova, so that actual proof of its affinity was not at first forthcoming. That proof was obtained in a very singular and unexpected manner. An example was taken by Behrens in 1902-3 on the west shore of Lake Victoria Nyanza, near Entebbe, and was described and figured by Professor Poulton in the Transactions of the Entomological Society in 1906. It proved to be a gynandromorphous specimen, the left wing exhibiting a considerable portion of the male colour and

¹ Trans. Ent. Soc., p. 283, 1906.

² Proc. Ent. Soc., 1903, p. xxxviii.

pattern. Not only is the pale yellow ground-colour of the male represented in a series of scattered markings over both the wings of the left side, but also a portion of the black sub-marginal border of the male hind-wing is plainly visible, as though superimposed on the dark brown portion of the female coloration. Such partially hermaphrodite specimens of various species are by no means unknown in collections, though always extremely rare; but probably no previous example has even borne such great scientific importance. Even the variety *planemoides* does not exhaust the known mimetic forms of *P. dardanus*. In his appendix to the Rev. K. St. A. Rogers's paper on British East African butterflies in the Trans. Ent. Soc., 1908, Trimen has described a form of the subspecies *dardanus tibullus*, which he has named *dorippoides*. This specimen is figured on Plate X, Fig 11, and, as will be seen, presents a remarkable resemblance to *chrysippus* f. *dorippus*. It would appear to be a modification from the *trophonius* form. The single specimen at present known was taken at Nairobi in 1893. Trimen points out that, in view of the tendency of *chrysippus* mimics to produce modifications towards its form *dorippus*, we should expect *dardanus* to have a corresponding form also; the absence of *dorippus* from West Africa and its rarity in the south would lead us to expect the appearance of a *dorippus*-like form in that region where *dorippus* is known to be common, and this is precisely what has been discovered in the *dorippoides* variety. No doubt further collecting experience will show that this variety is not so rare as the single example at present available would lead us to suppose.

Papilio dardanus evidently maintains its existence on the African continent entirely by its very remarkable adaptability to mimetic variation, for even in its larval and pupal stages it presents similar phenomena, the pupa even departing from the usual characteristics of its genus in order to accentuate the deception. In the account of the first breeding experiment already referred to, Mr. Mansel Weale described the early stages of the butterfly.¹ The larva feeds on *Vepris lanceolata* and in the earlier stages bears filamentous tubercles which probably resemble those of the larva of *Amauris echeria*. These tubercles grow longer as the larva increases in size up to the last stage, when they become very short, and the full-grown larva is very difficult to distinguish from the leaf. Following on the description referred to, Trimen contributed a paper² affording some further details of the early stages, and from these two sources we learn the following interesting particulars. The change from the larva to the pupa is a very singular process and is thus described: 'The caterpillar generally fixes its anal legs below the axil of a leaf-stalk, and fastens itself below the sixth segment with a double thread to the petiole; the whole body becomes flaccid and pale green, with an increase of white along the sides, the head curved upwards and inwards. In this state it invariably remains for about twenty-four hours. The body then contracts longitudinally, and the skin is gradually pushed backwards; when the skin of the head is detached, the bifid tubercles of the head, *which in this stage are widely separated*, are pointed upwards, and pushed against the suspensory threads; the antennae,³ which are detached from the rest of the body, are likewise bent upwards, and the united efforts of the tubercles and antennae push the loose skin between the suspensory threads. The body is then violently bent from side to side. The thread by which the anal extremity is attached is lengthened, so that it becomes almost detached, and the loose skin is then shaken off. After a slight pause, the fork of head becomes straightened, and the tubercles

¹ Notes on the Habits of *P. merope*, with a Description of its Larva and Pupa, J. P. Mansel Weale, Trans. Ent. Soc., 1874, p. 131.

² Observations on the Case of *Papilio merope*,

R. Trimen, Trans. Ent. Soc., 1874.

³ Mr. Weale, in a subsequent communication, expresses some doubt as to whether the antennae or the haustellum may be thus employed.

parallel. The body is at intervals drawn up at the thorax ; the head is drawn downwards and the antennae become attached to the body. The anal extremity is again attached. The keel and lateral ridges appear, and the bifid processes, which are now closely parallel, are bent downwards. The imago emerges in about three weeks.' Remarking on the very curious and exceptional function of the cephalic processes and the haustellum or antennae, Trimen points out the interesting fact that those organs which perform the function of conversion to the pupal stage are just those which afterwards contribute so much to the cryptic nature of the pupa. The haustellum represents the midrib of the leaf and the processes the apex. The pupa is so perfectly adapted to resemble the leaves amongst which it is found that it is only with the very greatest difficulty that it can be seen. It is much flattened and the lateral ridges are greatly developed. The ventral side is darker than the dorsal, though as it is placed with the ventral side uppermost it thus perfectly represents the lanceolate leaf, which is darker above than below. The cephalic processes, usually wide apart in pupae of this genus, are in this case contiguous, and represent the point of the leaf. So perfect is the resemblance that the same author records that even when attached to a bare mimosa twig it deceived several persons to whom he exhibited it. Mr. Leigh says¹ that the larvae feed on the lower parts of the plant, and though not so difficult to detect in the earlier stages, they are in the last stage 'the hardest larvae to find of any with which I am acquainted . . . the pupae are even harder to find than the larvae'. The same naturalist also furnishes the interesting information that the pupa of the *trophonius* form is distinguished by a number of brown lateral markings.

Whilst the female *dardanus* has adopted a variety of forms of disguise in order to escape her enemies, the male has to rely on his superior powers of flight. The female adopts the slow-flying habits of its models, and frequents the thick bush, whilst the male is found more in the open and is a strong and rapid flyer. As Mr. Weale remarks, 'nothing can be more remarkable than the difference of flight in the two sexes.' Physical activity would not, however, serve to protect the insect when at rest, and it is interesting to learn that it reverts to the subterfuges of its earlier stages and becomes extremely cryptic. The somewhat elaborate pattern of the underside as shown in Fig. 2 would not perhaps at first sight suggest invisibility, but when settled with the fore-wings dropped back within the secondaries, and the longitudinal markings accentuated by the tail, the insect becomes extremely difficult to observe. Thus, in a letter to Trimen² in 1871, Mrs. Barber wrote as follows: 'I caught a fine *merope* with my finger and thumb the other day. It was just beginning to rain, and, though it was not late, *merope* thought proper to seek a resting-place, which he wisely chose upon a shrub which resembled his own underside colouring. It was a splendid match : when he closed his wings amongst the yellow and brown seeds and flowers of the shrub, no bird would ever have distinguished him. I had no net with me, and my first attempt was a failure. However, the butterfly took a turn round the neighbourhood, examined several other shrubs (which he found not so good I suppose) and eventually returned to the same perch.' Surgeon-Capt. W. G. Clements, writing 'On a Collection of Sierra Leone Lepidoptera', 1893, notes a similar habit in the male of typical *P. dardanus*. He states, 'It almost invariably selects a broad-bladed grass, striped with brown and yellow, and hanging pendant from its extremity with the wings folded, the upper ones being covered over and concealed by the lower, it cannot be seen until it is again startled into flight.' It may be noted that Mr. Weale has observed a species of flycatcher chase and capture *P. merope*, as he records in the paper already referred to.

¹ Trans. Ent. Soc., 1904, p. 679.

² Trans. Ent. Soc., 1874, p. 145.

It now remains to give some account of the nomenclature of *Papilio dardanus* and its various subspecies, and to endeavour to reduce to some kind of order the mass of conflicting descriptions which have accumulated round this extraordinary butterfly.

PAPILIO DARDANUS HUMBLLOTI, Oberthür, Comoro I.

A primitive form in which the male and female closely resemble one another. The margin of all four wings is black without the broken appearance which characterizes the other forms. Judging by Oberthür's figures, these marginal bands are somewhat broader and darker in the female than in the male, whilst the black mark in the cell of the fore-wing is more pronounced, and the distal end is very sharply defined. This costal black band is a most important feature, as it forms the ground-work of the ultimate development of the mimetic features in the other forms. Also it is very remarkable that the clear definition of its distal extremity can be traced in practically every other female form. It would seem as though no amount of evolutionary change could cause dark scales to appear for a short distance beyond this point, and the resulting pale area forms one of the most perfectly consistent features throughout the entire race. It is more permanent even than the apical spot which occasionally disappears from some of the more greatly modified varieties.

PAPILIO DARDANUS MERIONES, Felder (= *brutus*, Boisduval), Madagascar, Pl. X, Fig. 1, ♀.

This subspecies is peculiar to Madagascar and has a female resembling the male except for the much greater development of the costal bar already referred to. In the example figured this marking nearly reaches the median nervure, but its distal end continues to be very sharply defined. In twelve examples of both sexes which I have examined there is a tendency in the females to a more ochreous ground-colour than in the male, whilst the dark areas are brown rather than black. The black markings on the male hind-wings are of a somewhat less indeterminate outline than in the same sex of other subspecies, though, owing to great variability, it would be difficult to separate them if mixed with those from other localities.

PAPILIO DARDANUS ANTINORII, Oberthür. Abyssinia, Somaliland.

It is in this subspecies that we first find polymorphic forms of the female. The male is characterized by the paucity of black markings on the hind-wings and generally somewhat smaller size. The typical female closely resembles that of *meriones*, especially in the development of the costal black bar. All the dark markings are again brown rather than black. To this subspecies belong the curious female forms *niavioides*, Kheil, Plate X, Fig. 4, and *ruspinae*, Kheil, Plate X, Fig. 8.

PAPILIO DARDANUS DARDANUS, Brown (= *merope*, Cram.). West Coast to Victoria Nyanza (= *sulfurea*, Palis. Beauvois = *brutus*, Fabricius).

In this subspecies the males, which vary within wide limits, are with difficulty distinguishable from those of other localities. There is no known female resembling the male, but the subspecies produces several mimetic varieties of which the principal are :—

f. **DIONYSOS**, Doubl. and Hewitson, Plate X, Fig. 7.

This, as has already been remarked, is either an intermediate variety or a reversion to some ancestral form.

f. **HIPPOCOON**, Fabricius, Plate X, Fig. 5.

This form mimics *Amauris niavius* of the west, and it is noticeable that the black margin of the hind-wing is broader than the *hippocoon* forms of the south and east, just

as *niavius* has a broader black border than its southern representative *dominicanus*. The example illustrated is also remarkable in the possession of rudimentary tails to the hind-wings. The pale area beyond the costal bar has become a spot corresponding to the cell spot of the model.

f. TROPHONIUS, Westwood, Plate X, Fig. 9.

The *trophonius* of the *dardanus* subspecies differs from that of the south by the strongly marked internervular rays in the hind-wing. It mimics *D. chrysippus*.

f. PLANEMOIDES, Trimen, Plate X, Fig. 12.

This mimic of *Planema poggei* occurs only where the model is common. We can still observe in this form the persistent retention of the pale area beyond the costal bar, now represented by a mere notch.

PAPILIO DARDANUS CENEA, Stoll. South Africa, Plate X, Fig. 2 (male). Transitional forms to *tibullus*, Kirby. Delagoa Bay to Mombasa. Male = *brutus*, Godart.

The males of this subspecies are generally, especially in the south, characterized by the greater extent and continuity of the black submarginal border in the hind-wings, and also frequently by the much darker shade of the complicated underside pattern. Female forms associated with it are :—

f. HIPPOCOON (= *hippocoonides*, Haase), Plate X, Fig. 6.

Distinguished by the narrower hind-wing margin corresponding to that in the model *niavius dominicanus*. Intermediate forms figured by Hewitson have been described as *niobe* and *nioboides* by Aurivillius.

f. TROPHONIUS, Westwood, Plate X, Fig. 10.

Distinguished from the western *trophonius* by the faintness and attenuation of the dark internervular rays in the hind-wing.

f. CENEA, Stoll., Plate X, Fig. 13 (buff-spotted), Fig. 14 (white-spotted).

This form is by far the commonest of all varieties of female, and mimics the white and buff-spotted forms of *Amauris*. It is very unfortunate for the simplicity of the nomenclature that in this case we have the same name for a subspecies and also for a variety which is common to other subspecies, and this fact must be born in mind when dealing with the forms of this butterfly. The full designation of this variety consequently becomes *Papilio dardanus cenea*, form *cenea*.

PAPILIO DARDANUS TIBULLUS, R. and J. Delagoa Bay to Mombasa.

This subspecies is less distinctly separated from *dardanus cenea* than are the other forms, intergradations being commonly met with, but as it has been given subspecific rank I have included it here. It has the following forms of female :—

f. HIPPOCOON.

f. CENEA (buff-spotted).

f. CENEA (white-spotted).

f. TROPHONIUS.

f. TRIMENI, Poulton.

The *trimeni* form occurs also in the subspecies *polytrophus*, but is larger in *tibullus* than in the former.

DORIPPOIDES, Trimen, Plate X, Fig. 11.

This peculiar form already described is at present but little known, and may be found to occur in other subspecies. It mimics *D. chrysippus dorippus*.

PAPILIO DARDANUS POLYTROPHUS, R. and J.

This subspecies is found on the Kikuyu Escarpment. The individuals are distinguished by their generally smaller size. It has the following female forms:—

HIPPOCOON.

TRIMENI, Plate X, Fig. 3.

CENEA, Plate X, Fig. 15.

PLANEMOIDES

TROPHONIUS.

The *trimeni* form, as has already been described, is the least modified of all the female varieties. Professor Poulton is of the opinion that it is from this form that all the other female varieties have been derived.¹ Certainly all the other forms can be easily traced through a series of slight modifications from this variety.

In *Papilio dardanus* the phenomenon of butterfly mimicry, not only in its existence, but in its development, is beautifully illustrated. In Grand Comoro we have a primitive form remaining in which the female only differs from the male in the slightly greater development of the costal black bar. In Madagascar this marking has become larger and extended towards the median nervure. The same feature appears in the Abyssinian form *antinorii*, which has also produced two other varieties which throw a curious light on the possibilities of mimetic development. We then have the *trimeni* form of female, and in a series of examples of the subspecies *polytrophus* the gradual change can be seen through *trimeni* to *cenea* on the one hand and to *hippocoon* on the other. It is of no consequence whether *trimeni* be a survival of an early stage or a reversion, it remains an intermediate form and shows what small changes may produce a beneficial resemblance to some suitable model. *Hippocoon* may develop reddish-brown basal areas together with other smaller modifications and the butterfly resembles *chrysippus*, or the dark areas may extend in imitation of *Amauris*, or give place to a pale brown suffusion producing *dorippoides*. A modified *hippocoon* develops yellow only on the fore-wings, and the *planemoides* form is produced. The male, with his more powerful flight, is hidden when at rest by a perfect adaptation of cryptic coloration. The early stages are protected by the same means, so that the larvae are most difficult to find, and the pupae almost indistinguishable from leaves. The whole life-history of *dardanus* is an illustration of the keen struggle for existence which is met by a development of mimetic modification unparalleled in any other species with which we are acquainted. The most earnest opponent of mimetic theory cannot deny the resemblance of the pupa to a leaf, or that of the male, when at rest, to its surroundings. Why are *Amauris echeria*, *albimaculata*, and *niavius*, *Danaida chrysippus*, and *Planema poggei* unusually common butterflies, if not by reason of some advantage which they enjoy in their relation to vertebrate enemies, and how is it that out of the unlimited number of patterns which an unstable form like *dardanus* might produce, the principal varieties happen to be those which most resemble these plentiful and slow-flying species? These are problems for which the opponents of mimicry will have to find some much better explanation than those of climatic influence, sexual selection, and parallel variation, before we can see any good reason to abandon Bates's comparatively simple and wholly reasonable explanation.

¹ Trans. Ent. Soc., 1906, p. 288. Regarded in strict order of evolution this subspecies might preferably have been inserted on p. 99, after *P. dardanus antinorii*.

NOTE. Since the foregoing account was written my attention has been called to a paper by Professor Aurivillius published in 1907, and dealing with some forms of *P. dardanus*. The principal object of the paper seems to be to give names to several of the intermediate varieties and aberrations of this insect. Any work published by the eminent Swedish naturalist to whom we owe so comprehensive and valuable a work as the 'Rhopalocera Aethiopica', is sure of a welcome from those who, like myself, owe so much to his exemplary labours, and the reason why I have not rewritten this section of my work and inserted the additional names is because it seemed to me that the nomenclature of the forms of *P. dardanus* has already, from the nature of the case, assumed a complication of such proportions, that my foregoing effort to state the case as concisely as possible would be to some extent defeated were I to add the proposed names for the intermediate varieties. *P. dardanus* is an extremely unstable species, and this, combined with the possibility of intercrossing of the principal varieties which have become fairly well established, makes the occurrence of intermediate aberrations a frequent possibility. In the Hope Department at Oxford there are many unique forms, and there are two in my own collection of which I have never seen duplicates. Several of these intermediates, including one of my own specimens, have been described (though not named) by Professor Poulton (Trans. Ent. Soc., 1906). Professor Aurivillius's paper contains figures of an intermediate form between *trimeni* and *dionysos*, two intergrades from *trimeni* to *hippocoon*, a form between *hippocoon*, *trimeni*, and *cenea*, a variety between *hippocoon* and *planemoides*, and two *hippocoon* forms from Ukerewe Island in Lake Victoria Nyanza. A table is also given which includes seventeen varietal names, including those given in the foregoing account. The paper is in the Arkiv für Zoologi, Bd. 3, No. 23 (1907), and is published in London by W. Wesley and Son, Strand.

AN ACCOUNT OF SOME OTHER APPARENT INSTANCES OF MIMICRY NOT FIGURED ON THE PLATES

I have now described a large number of the most striking instances of mimetic association in African butterflies, but the very wide extent to which this phenomenon occurs makes the task of figuring all the known examples one which would require several supplementary plates. Some account, however, of certain further instances may be of service. It has already been noticed that some specimens of the male *Euxanthe wakefieldi*, Ward, bear a certain resemblance to *Tirumala petiverana*. I have lately seen a specimen of this species which was taken in company with the Danaine, and in which the ground-colour is much more inclined to brown than to the usual intense black, whilst the green markings are duller, the whole effect being to produce a much closer approach to *T. petiverana* than in any example which I had previously examined. The existence of this variety convinces me that the species is in fact approaching the Danaine pattern. As so frequently happens, the female has made much greater strides towards the pattern of a protected species. In this sex the markings are all white, and by their concentration in the fore-wings into a more or less well-defined sub-apical bar and a discal patch, and in the hind-wings into a large basal white patch, a very close resemblance to *Amauris ochlea* is produced. The Rev. K. St. A. Rogers, in his paper in Trans. Ent. Soc., 1908, says that the species when on the wing bears a closer resemblance to the *dominicanus* type than to *ochlea*. The same author expresses the opinion that the female *Euxanthe tiberius* is also a member of the combination, and that, judging from the slowness of their flight and the toughness of the integuments, these species are Müllerian rather than Batesian mimics.

Many members of the genus *Neptis*, which are nearly all small black and white butterflies, are accompanied in their flight by species of *Neptidopsis*, a Eurytelid genus founded by Aurivillius. Thus the common *Neptis agatha* is frequently accompanied by *Neptidopsis ophione*, which very closely resembles it, and also by a small black and white day-flying moth of the genus *Nyctemera*.

A Nymphalid genus, *Pseudathyma*, Staud., doubtfully distinguishable from *Euptera*, contains a species, *neptidina*, Karsch, which in pattern and markings is almost indistinguish-

able from *Neptis lermanni*, Auriv., and both are described from the Congo State. They are figured together on Plate I in 'Rhopalocera Aethiopica'.

Neptis woodwardi, E. M. Sharpe, is an interesting form which presents a distinct approach to the *Amauris echeria* and *albimaculata* association, having an ochreous bar on the hind-wings and white spots on the primaries. The connexion of this species with the *albimaculata* group was indicated by Neave in Trans. Ent. Soc., 1906, p. 214, and examples from Kikuyu and the north-east shore of Lake Victoria Nyanza have been examined by Professor Poulton (see Trans. Ent. Soc., 1908, p. 512) who shows that the more eastern examples, coming from a country where the influence of the Danaines is at its strongest, have larger white spots on the fore-wings, and the ochreous band on the hind-wing is very much more developed, almost amounting to a patch in the female. In both localities the females show a greater modification towards the Danaine pattern than do the males.

An Acraeine appearance is presented by the underside of the Lycaenid *Catochrysops mashuna*, which has a pale tawny ground-colour and a number of black spots causing it to resemble *Acraea encedon*. Several *Hesperidae* have also a marked Acraeine appearance on the underside, notably *Abantis tettensis*, *Kedestes macomo*, and *Baoris netopha*. The bright orange-coloured Lycaenid, *Deloneura millari*, Trim., as also the *D. immaculata* of the same author, resemble certain Liparid moths. *D. millari* is figured and described by Trimen in Trans. Ent. Soc., 1906, p. 69, together with the moth *Euproctis punctifera*, Walk., with which it is associated. Mr. Millar, who took the insects together, states that the moth and butterfly are quite indistinguishable on the wing, both the flight and appearance being the same. The insects occur at Durban and the author notes that the butterfly has evidently hitherto escaped observation by its resemblance to this common moth.

The moth *Aletis helcita* is often accompanied by the Hypsid moth *Phaegorista similis*, Walk., as previously noted, and also by a species of *Neuroxena* which closely resembles it. In the former the hind-wing is without the white spots, but the effect is obtained by white internervular marks on the fringes. The latter species has a small black spot in the discal area of the hind-wing.

A very remarkable species of moth, *Hibrildes neavei*, Hampson, is bisexually mimetic and corresponds to the two sexes of *Acraea anemosa*. *Pentila kirbyi* is accompanied at Sierra Leone by a moth of the genus *Geodena*. The latter is white with a black spot in the middle of each wing, and mimics the Lycaenid very closely.

Further knowledge of the African Lepidoptera will doubtless bring to light many new instances of mimetic resemblance. Many species of the closely allied genera *Euphaedra* and *Euryphene* resemble each other very closely, whilst some species of *Charaxes* appear to have polymorphic forms of female which resemble other species of the same genus. These cases are, however, extremely intricate, and it would be premature to attempt to deal with them at the present time, and we may therefore pass on from the foregoing descriptions to certain further considerations of the subject as a whole.

ON OBJECTIONS WHICH HAVE BEEN RAISED TO THE THEORIES OF MIMICRY, AND THE EVIDENCE ON WHICH SUCH THEORIES ARE BASED

WE have seen that Bates's original theory of mimicry included an explanation of the cause of the phenomenon, and its author did not deem it necessary to do more than state the facts of these resemblances as illustrative of the Darwinian principles. Probably few, if any, of those who have studied the subject at all, would be prepared to make any attempt to disprove the statement that mimicry does in fact exist, whatever may have been the cause from which it originated. More especially will it come as something of a surprise to those who have carefully followed the descriptions in the foregoing pages and examined the figures comprised in the accompanying plates, that in order to deal fully with the subject, we must, so to speak, go behind our title and emphasize the very existence of mimetic resemblance before attempting to find a cause for its development. Nevertheless R. H. Lock, in his work 'Variation, Heredity, and Evolution', dismisses the whole subject with the remark that 'Several supposed examples of this phenomenon have been described in the case of different genera of tropical butterflies'. I am content to allow the previous 79 pages and the 173 figures on the plates to appear in support of the above perhaps rather inadequate statement, though it may be as well to point out that this work deals only with 'several supposed examples' in the Lepidoptera of the Ethiopian region, and that, had space and the cost of lithography permitted, I might have figured and described a large number of the diurnal Lepidoptera of the Oriental and Neotropical regions in support of the preliminary contention that the phenomenon of mimetic association is one the existence of which cannot longer be held in dispute.

Having so far established the basis of discussion, we may, I think, fairly proceed to consider more fully the question as to how such mimetic associations have been brought about. It has already been stated that natural selection affords a more complete explanation of mimicry than do any of the alternative suggestions which have at various times been put forward. It may be at once stated, however, that alternative theories are neither numerous nor greatly developed, and whilst the Batesian and Müllerian theories based on natural selection, and including their more recent elaborations and extensions, have been frequently doubted and in many cases refused altogether, none of those who have openly stated their disbelief in these theories have been able to offer any alternative explanation which would suffice to account for the cases of mimetic coloration with which we are acquainted. Those who have read the introductory portion of this work will be in a position to appreciate such criticisms as have been put forward, so that we may at once proceed to enumerate the objections which have been thus proposed, and consider the limitations to which such objections are liable, after which it will be possible to fully consider the extent to which the theory of natural selection is supported by observation and experiment.

The late W. C. Hewitson was one of the first to record his lack of faith in these principles. We have already seen how impossible of belief he found Trimen's theory concerning the female forms of *P. dardanus*, though probably few naturalists have ever given such a peculiarly unscientific reason for their views. Hewitson's objections do not in fact demand serious consideration, since, in common with many others who have criticized Darwin's theories, he does not appear to have understood the principles in which he professed disbelief. Further reference would be unnecessary were it not for the fact that in his 'Exotic Butterflies' there occurs a passage which reads as follows: 'May not all the imitators of these scented aristocrats be simply votaries of fashion, aping the dress of their superiors, and, since the females take the lead, "naturally selecting" those of the gayest colours.' It is worthy of note that there is a suggestion in this passage which at first sight appears to be a kind of dim perception of the idea of sexual selection, though it is doubtful whether this was the writer's intention, and it more probably suggests a kind of conscious selection of certain colours on the part of the females for their own adornment, a process which is no more credible than that a man can 'by taking thought add one cubit to his stature'. The late Dr. Fritz Müller was the first to advance the idea of sexual selection, the principle of the theory being that the comparatively rare mimic, being surrounded by large numbers of the model, might come to appreciate the colours which were thus so frequently displayed before it, and so prefer, in pairing, to select individuals of its own species which by variation tended to exhibit those colours in the highest degree. By this means the resemblance to the model or dominant form would be increased and perpetuated. The suggestion was made in a letter to Darwin in 1872. The latter considered the theory as rather too speculative, although at the time he inclined to the idea that it was not as incredible as might at first sight appear.¹ Sexual selection is not, however, sufficient to account for many of the resemblances with which we are now acquainted, such, for instance, as the polymorphic forms of *P. dardanus*; nor would this explanation have any weight in the case of the resemblance of a larva to a snake, or that of the pupa of the Magpie moth to a wasp.

In 1897 a most interesting discussion took place during the first two meetings of the Entomological Society of London, when the subject of mimicry was dealt with by many of the Fellows. The discussion followed the communication of Dr. Dixey's valuable paper on 'Mimetic Attraction', and the exhibition by Mr. Blandford of groups of butterflies from the Neotropical region, such groups exhibiting what Mr. Blandford described as 'homoeochromatism', the term being used in order to express the phenomenon of what is known as Müllerian resemblance, without implying any theoretical considerations as to its origin. In explaining the exhibit, it was pointed out that some of the resemblances were so close as to be of the nature of hypertely,² and that the selective force could scarcely be considered adequate to produce such perfection in minute details. In the case of many of the resemblances it was pointed out that there was nothing to show that identical conditions might not have brought about identical results in the matter of variation of colour patterns. In this case the explanation suggested appears to have been that of parallel variation. The remoteness of the possibility of two butterflies, or any two other creatures, arriving at the same result by a process of parallel variation has only to be considered in order to be rejected. If the influences which give rise to variation, and the controlling forces which select certain

¹ See 'Charles Darwin and the Theory of Natural Selection,' Poulton, London, 1901.

² This term was proposed by B. von Wattenwyl (Verh. Zool. Bot. Ges. Wien., 1883, p. 248) to

express the idea that certain resemblances such as those of the tegmina of leaf-like *Orthoptera*, were so perfect in detail as to be beyond the limits of usefulness.

variations and reject others were both simple in nature and regular in action, such a consummation would be difficult of attainment ; but when it is considered that the factors which guide evolution are infinitely complex in their nature and varied in their incidence, it is plain that the probability of such influences following identical lines through a long course of evolutionary change, and so arriving ultimately at the same result is to the last degree remote. Slight resemblances may doubtless be found between butterflies which inhabit widely separated regions of the globe. It would be rash to assert that in the multiplicity of patterns which these insects present, no butterfly, say in South America, bears the least resemblance to any Asiatic form. Such a resemblance, if it exists, is not, however, of the kind of which this study treats. It is not governed by the patterns of dominant species forming mimetic associations coincident in time and place. To attempt to account for the known instances of mimicry by parallel variation, would be to argue that through the whole course of the evolution of model and mimic, the influences which have on the one hand produced profound differences of anatomical structure, have on the other hand contradicted their own evident diversity by producing the same pattern, and combined this unlikely result with the strange coincidence that the pattern so selected happens also to be that of a species which is more or less distasteful to its enemies. In spite of the large amount of proof now obtained of the comparative distastefulness of many insects, there is not yet any instance recorded where the dominant form of a mimetic association has proved to be highly relished by insectivorous foes.

In the course of the discussion referred to, the danger was pointed out of mistaking for mimicry resemblances which were in reality due to consanguinity. It was also urged that too much stress had been laid on the supposed destruction of butterflies in the imago state, and that the greatest destruction took place in the earlier stages, also that proof of the inedibility of the so-called models was still required. The rarity of observed cases of the attacks on butterflies by birds was insisted upon by many of the speakers, especially those qualified by considerable collecting experience to express an opinion on this point, and finally climatic influence was suggested as a potent cause for the development of similarity of pattern. As regards proof of the inedibility of protected species, ample evidence has now been accumulated, thanks to the extensive experiments of G. A. K. Marshall, Professor Poulton, Professor Weismann, and others. Many of these experiments are described later.

A very extensive criticism of the Batesian and Müllerian hypotheses appeared in 1904 in a paper by the late Professor Packard.¹

This essay was criticized at some length by the present writer in a paper communicated to the Entomological Society of London in 1906,² when it was pointed out that the author's arguments were to a great extent based on wrong premisses. His conception of Müller's hypothesis was incorrect owing to his having mistaken the suggestion of sexual selection made by Müller for the accepted Müllerian hypothesis, an error which was pointed out by Professor Meldola in a letter to 'Nature' in 1905.

The view of Mr. Abbot H. Thayer, that the colours of animals are such as to cause the creatures to become invisible, and which Professor Packard supports, is merely a universal adaptation of the theory of cryptic coloration, and cannot be applied to the numerous instances of warning colours with which we are familiar.

¹ Proc. Amer. Phil. Soc., 1904: 'On the Origin of the Markings of Organisms due to the Physical rather than to the Biological Environment, with Criticisms of the Bates-Müller Hypotheses,' A. S. Packard, LL.D.

² On the late Professor Packard's paper 'On the Markings of Organisms', Eltringham, Proc. Ent. Soc., 1906, p. xxxvii et seq.

The next point insisted on was the paucity of recorded instances of attacks on butterflies by insectivorous birds. Until recently this argument has not been without some justification. There has, however, been recently communicated to the Entomological Society of London an extremely valuable and interesting paper by Marshall, giving a collection of instances in which birds have been observed to eat butterflies,¹ together with certain very potent arguments on the subject which will be referred to later.

Much stress was laid by Professor Packard on the explanation that resemblance between butterflies is due to similarity of environment. This view, however, becomes untenable when applied to resemblance between insects of different orders, and the environments of which, in the early stages, the only ones which affect the ultimate pattern, are in many cases very different.

The only other important criticism which has come to the writer's notice is that contained in the 'Cambridge Natural History'.² The principal points here insisted upon are, (1) that the phenomena are supposed to have occurred in the past, so that they cannot be directly verified or disproved; (2) that birds do not destroy butterflies in the perfect state; (3) that an amount of resemblance in the model that is assumed to be efficient at one step of the development, and to bring safety, is at the next step supposed to be inefficient and to involve destruction; (4) that there is no sufficient evidence that the species which are now similar were ever dissimilar.

The first objection is not only a criticism of the special theory of mimicry, but amounts to a complete repudiation of evolutionary theory in general. The upholders of the Bates-Müller theories maintain that natural selection is the governing force which has produced and is producing mimetic phenomena, and probably no naturalist, least of all the distinguished author of the section 'Insecta' in the 'Cambridge Natural History', would be prepared to maintain that natural selection, if it ever affected butterflies in the past, has now ceased to affect them. We cannot expect to see the process of selection actually and visibly taking place, but we have remarkable evidence of the influence of the recent invasion of a foreign species on the indigenous forms of *Limenitis*.³ It is therefore quite inconsistent with evolutionary theory to suggest that mimetic resemblances are no longer in process of development.

The evidence as to the attacks by birds is dealt with later at greater length.

In reference to the third objection, it should be pointed out that the amount of resemblance which first gives an advantage to its possessor is not assumed to bring safety, but merely a slight advantage in the struggle, which advantage is liable to be increased and perpetuated by further selection and more perfect resemblance. It is to be feared that the inappropriate use of the word immune as applied to protected species is responsible for many similar misconceptions as to the precise nature of the advantages which dominant forms enjoy. It is not maintained that any species, however well protected, is immune from one kind of attack or another. Real immunity in any species would bring about such an increase in the number of individuals that the world would speedily become uninhabitable for those creatures whose numbers remained at a normal figure. The contention is rather that certain species are less destroyed by their natural enemies than are others. A slight but recognizable modification in the appearance of a more palatable form in the direction of one less palatable will convey to the former a comparatively better chance of survival, but it does not bring immunity, and hence the modification remains capable of

¹ 'Birds as a Factor in the production of Mimetic Resemblances among Butterflies.' G. A. K. Marshall, Trans. Ent. Soc., 1909, p. 329-83.

² Insecta, Part II, p. 337, et seq.

³ 'Mimetic North American Species of the Genus *Limenitis*,' Poulton, Trans. Ent. Soc., 1907, p. 447-8.

still greater perfection. The model which makes such variation advantageous is not itself immune, for though plentiful by reason of its comparative paucity of enemies, it yet has its destroyers also, which keep within bounds what would otherwise be its ever-increasing swarms. A species which has developed qualities which protect it from one form of enemy may be exterminated by another pursuer which has itself developed special faculties for effective pursuit. As has already been stated, we see only the present survivals, the forms which are enjoying, perhaps only temporarily, the results of successful variation.

Dr. Sharp's third objection, although it is actually aimed at the theory of mimicry, applies equally well to the progressive stages in the evolution of any organ or structure in animals or plants: it is, in fact, only an objection to mimicry in so far as it is an objection to adaptive evolution of any kind.

The fourth objection merits but little consideration. One of the most noticeable features of the mimetic developments already illustrated is the manner in which the mimetic species have departed from the normal pattern and coloration of their own genera, in order to resemble the forms which serve as their models. To pursue this objection to its logical conclusion would involve the assertion of the original creation of all the butterflies exactly as we now see them, a suggestion which can hardly have been intended by the writer. We thus see that three out of Dr. Sharp's four objections are criticisms of evolutionary theory in general, and are not specially applicable to the theory of mimicry.

We may now consider the basis on which the natural selection theory is founded. In order adequately to support this view, there are two main contentions for which justification must be found, namely, first, that some butterflies are less palatable to insect-eating enemies than are others, and second, that butterflies are in fact preyed upon in the imago state by birds and other insectivorous foes; and further, that young birds do not instinctively know what to eat and what to avoid.

III

ON THE EVIDENCE THAT SOME BUTTERFLIES ARE MORE PALATABLE THAN OTHERS

IT has been seen that one of the objections which has been raised against mimetic theories is that there is insufficient evidence that the so-called protected species are in fact unpalatable. It was on the assumption of the unpalatability of certain forms that Bates founded his theory of the mimetic resemblances to which he called attention in his original memoir already described in our introductory chapters. In inquiring what advantages the *Heliconidae* possess to make them 'so flourishing a group, and consequently the objects of so much mimetic resemblance', he remarks that they are probably unpalatable to their enemies. He observes that 'recently killed specimens of the Danaoid *Heliconidae*, when set out to dry, were always less subject than other insects to being devoured by vermin. They all have a peculiar smell. I never saw the flocks of slow-flying *Heliconidae* in the woods persecuted by birds or dragonflies, to which they would have been an easy prey, nor when at rest on leaves did they appear to be molested by lizards or the predaceous flies of the family *Asilidae*, which were very often seen pouncing on butterflies of other families'.

Trimen's paper on 'Mimetic Analogies among African Butterflies'¹ was published in 1869, and gave strong confirmation of Bates's view that some insects are distasteful. On this subject he writes as follows: 'The peculiar smell noticed by Mr. Bates in the Heliconide *Danaidae* is also possessed by the *Euploea* of the Eastern Archipelago, as Mr. Wallace has recorded; and I am enabled to add similar evidence as regards the African species of *Danais* and *Acraea*. (The Mauritian *Euploea euphone* also gives out a strong odour when handled.) Judging from the case of *Acraea horta*, a widely distributed African species, which I have reared in considerable numbers from the young larvae, this disagreeable smell is not peculiar to the imago condition, but attends the insect throughout its life, even the pupae emitting it. On pressing the thorax of a *Danais*, a *Euploea*, or an *Acraea*, however slightly, a clear yellow liquid similar to that secreted by the Ladybird beetles, almost always exudes from that part of the body: and in some species of the two former genera a pair of bright yellow fascicled appendages are protruded from the extremity of the abdomen. The peculiar scent appears chiefly to reside in this liquid, being remarkably stronger with each effusion. Most of the species of *Danais* and *Acraea* feign death very readily; and they possess another means of defence which, as far as I am aware, has not hitherto been recorded, viz. the remarkable elasticity of their entire structure. No pressure of the thorax, short of absolute crushing of the tissues, suffices to kill or even paralyse these butterflies; and the collector who treats them as he would species of other families, soon finds his collecting-box alive with struggling occupants. . . . It is not difficult to perceive how important, as a reserve means of defence, this unusual elasticity of structure may prove. That birds and other eaters of insects may occasionally capture a butterfly of these malodorous tribes before discovering its distasteful character is not an unreasonable supposition, especially in seasons when an exceptional scarcity of food may prevail. In such a case it may be safely stated that the chances are very greatly in favour of a *Danais* or an *Acraea* escaping, if not wholly unhurt,

¹ Trans. Linn. Soc., vol. 26, pt. iii, 1869.

yet without serious injury, after rough treatment that would have proved fatal to a harder but less elastic animal.'

Wallace, in 'Natural Selection in Tropical Nature', gives considerable evidence as to the unpalatability of many butterflies. In speaking of the *Heliconidae* he says, 'These beautiful insects possess, however, a strong pungent and semi-aromatic or medicinal odour, which seems to pervade all the juices of their system. When the entomologist squeezes the breast of one of them between his fingers to kill it, a yellow liquid exudes which stains the skin, and the smell of which can only be got rid of by time and repeated washings. Here we have probably the cause of their immunity from attack, since there is a great deal of evidence to show that certain insects are so disgusting to birds that they will under no circumstances touch them. Stainton has observed that a brood of young turkeys greedily devoured all the worthless moths he had amassed in a night's "sugaring", yet one after another seized and rejected a single white moth which happened to be among them. Young pheasants and partridges, which eat many kinds of caterpillars, seem to have an absolute dread of that of the common currant moth, which they will never touch, and tom-tits, as well as other small birds, appear never to eat the same species. In the case of the *Heliconidae*, however, we have some direct evidence to the same effect. In the Brazilian forests there are large numbers of insectivorous birds—as jacamars, trogons, and puffbirds—which catch insects on the wing, and that they destroy many butterflies is indicated by the fact that the wings of these insects are often found on the ground where their bodies have been devoured. But among these there are no wings of *Heliconidae*, while those of the large showy *Nymphalidae*, which have a much swifter flight, are often met with. Again, a gentleman who had recently returned from Brazil stated at a meeting of the Entomological Society that he once observed a pair of puffbirds catching butterflies which they brought to their nest to feed their young; yet during half an hour they never brought one of the *Heliconidae*, which were flying lazily about in great numbers, and which they could have captured more easily than any others. It was this circumstance that led Mr. Belt to observe them so long, as he could not understand why the most common insects should be altogether passed by.'

The single white moth above referred to was *Spilosoma menthastri*. Jenner Weir found that this moth was refused by the bullfinch, chaffinch, yellow-hammer, and reed-bunting, though it was eaten after considerable hesitation by a robin. Amongst beetles the same experimenter found that the common Malacoderms (*Telephorus*) known as 'soldiers and sailors' were invariably refused by birds. Mr. Weir communicated the results of his extensive experiments to the Entomological Society in two papers on the relation between the colour and edibility of Lepidoptera and their larvae (1869 and 1870). He found that his birds would not eat hairy caterpillars, or any that were highly coloured and conspicuous in their habits, such as those of the Magpie or Currant moths, but that 'all caterpillars whose habits are nocturnal, which are dull coloured, with fleshy bodies and smooth skins, are eaten with the greatest avidity. Every species of green caterpillar is also much relished. All Geometrae whose larvae resemble twigs as they stand out from the plant on their anal prolegs, are invariably eaten'.¹ A. G. Butler also contributed, in 1869, a paper entitled 'Remarks upon some Caterpillars which are unpalatable to their Enemies'. Butler's observations confirmed those of Weir. Lizards and frogs, which would greedily eat caterpillars, flies, and even bees, would not eat the larvae of the Magpie and Burnet moths, and also that of *H. wawaria*, which they frequently seized but always rejected. Spiders also rejected such larvae. Professor Weismann experimented with lizards and birds and found that they refused

¹ These generalizations require some modifications in view of the experiments of Professor Poulton and others.

many brightly-coloured larvae, such as the Cinnabar, Buff-tip, and large Cabbage butterfly. I have myself to some extent confirmed these experiments with *Lacerta viridis*, which I found would eat most green caterpillars, and also the inconspicuous larvae of *T. pronuba*, but would only eat the larvae of *P. brassicae* with reluctance and when hungry. In 1887 Professor Poulton contributed a paper to the Proceedings of the Zoological Society on 'The Experimental Proof of the Protective Value of Colour and Markings in Insects in reference to their Vertebrate Enemies'. The experiments described were conducted with green tree-frogs and various lizards, and the results are of the greatest importance, since the inquiry was undertaken with the view of discovering how far the experiments would support (1) Wallace's suggestion that brilliant and conspicuous larvae would be refused by some at least of their enemies, and (2) the investigator's own suggestion that a limit to the success of this method of defence would result from the hunger which the success itself tends to produce. Putting the latter suggestion into other words, distasteful and conspicuous species might be eaten, albeit with reluctance, under the stress of hunger caused by the distasteful qualities themselves, such qualities thus becoming a limiting factor in the development of this means of defence. The experiments went even further than this. It was sought to prove the converse of Wallace's suggestion, viz. that all inconspicuous and cryptic forms would be eagerly devoured.

The details of the experiments are given in the form of tables which show in parallel columns the results of all the tests made by Jenner Weir, Butler, Weismann, and Poulton. Space does not permit of the reproduction of these exhaustive tables, but the results arrived at are most conclusive. Some eighteen species of lepidopterous larvae, all very conspicuous, were with one exception refused by some or all of the animals to which they were given, except in cases where the latter were very hungry. Then the larvae were eaten with evident compunction. The case of the larva of *V. urticae* was peculiar, as it was refused by birds but eaten by lizards, showing, as might be expected, that protection against one enemy is not always equally efficient against another. The distasteful qualities of the larvae of *A. grossulariata* would seem to be exceptionally well developed. Frogs would taste them, but always rejected them. A hungry lizard chewed one for some time and then rejected it. Birds also refused them. Jenner Weir's diary contains a note on this species, to the effect that a lizard which seized the larva immediately dropped it, afterwards licking its jaws as if to remove the unpleasant taste, whilst another lizard rubbed its nose and mouth against the moss after trying to eat one of these insects. Professor Poulton's further experiments on the behaviour of insectivorous animals towards inconspicuous and cryptic insects, for the most part supplied confirmatory evidence that such insects are readily eaten. The pupae of *Tryphaena pronuba* were eagerly consumed by his lizards, and he points out that the imago is much pursued and eaten by birds, a fact which I have myself frequently observed. It may be interesting to note, as evidence of the keen struggle for existence experienced by this species, that I have observed a female ovipositing while an earwig was eating the eggs as fast as they were laid. The most striking result of these experiments is, however, that they demonstrated the fact that some larvae, though exceedingly well concealed, nevertheless are highly distasteful. This phenomenon was illustrated in the case of the larva of *Mania typica*. It was immediately attacked by a lizard, but rejected after being severely bitten, and other lizards tasted the larva with the same result. As the author tells us, the young larvae, when hatched, devour the upper cuticle and parenchyma of the leaf, leaving the lower cuticle entire, dry, and brown. They lie closely packed side by side and apparently motionless, but in reality gradually leaving a large brown space behind, thus adapting the surroundings to the brown

colour of the larvae. The gregarious habits are subordinated to cryptic ends, affording a peculiar method of concealment for the young larvae. After a time, being too large to be further concealed in this manner, they descend and feed on low-growing plants. After hibernating they begin feeding again in the spring, always carefully concealing themselves by day, hiding themselves in the folds of brown leaves and in dark corners. In spite of the fact that the larva behaves in the same manner as those which are very palatable, and therefore must hide from their enemies, it obviously possesses a very nauseous taste and probably smell. The lizard recognized it as something which was expected to be palatable, and it was only after severely biting it that the nauseous taste became evident. Thus we have nauseous qualities present in a larva as an entirely useless attribute, a discovery of the greatest importance, for here at once is a possible explanation of the manner in which distasteful qualities may have arisen and become coupled with warning coloration. The distastefulness is there incidentally and should the struggle for existence become so severe as to cause the larva in its hiding-place to be more carefully sought by its foes, we can easily understand how selection, acting on variation, might develop a pattern which would be conspicuous and easily recognized, thus causing a change in the creature's mode of defence. It is further pointed out by the author of the experiments that there is no known instance of an insect being distasteful in the imago state when the larva is edible, showing that the distasteful qualities have evidently arisen in the larval stages. This is certainly what we should expect, since the nauseous juices are probably elaborated from the food plant, and thus passed on to the pupa and imago. The author gives a list of special conclusions which may be drawn from the results of the foregoing experiments. Those bearing directly on the present subject are—

1. Highly conspicuous insects nearly always possess some unpleasant attribute, i.e., a disagreeable taste or smell in the tissues or fluids of the body, or (in the case of the smell) discharged from special glands: irritating hairs or stings.
2. In a small number of cases a highly conspicuous appearance has not yet been shown to be attended by any unpleasant attribute.
3. The likes and dislikes of insect-eaters are purely relative, and if pressed with hunger the most disagreeable and highly conspicuous insects may be eaten. Hence probably the relatively small number of species which adopt this mode of defence.
4. In a very small number of species the most perfect form of protective resemblance may coexist with a most unpleasant taste.

It was in the hope of making some further discoveries in regard to the edibility of larvae that I undertook in the summer of 1909 some experiments with lizards. A species of green lizard, probably *Lacerta viridis*, was utilized for the purpose, and my results were communicated to the Entomological Society in October of that year. Generally speaking, the results confirmed those of previous experimenters. Green larvae and all those which were inconspicuous, and for the most part night feeders, were eagerly devoured. Blue-bottles and other flies were always relished. Once a bee was seized, but the lizard was evidently stung as it dropped the insect hurriedly. The most interesting result was obtained with the larva of the Geometrid moth *Odontopera bidentata*. This larva is probably better protected by a cryptic appearance than almost any other British species. I found it feeding on ivy, and so perfect was the resemblance of the caterpillar to the ivy twigs that in many cases it could only be detected by the sense of touch. Nevertheless my lizards found it extremely distasteful. They would seize the larva and drop it again with every sign of disgust. They rubbed their noses on the gravel at the bottom of the cage, and in one case a lizard which had had no food for some days apparently managed to swallow the caterpillar.

A moment afterwards, however, it ejected it and ran violently round the cage, finally drinking some water. In the course of a great number of trials the larva was actually eaten on one or two occasions, but usually under stress of hunger or competition. Once two lizards seized the same larva, which was pulled in two in the fight which ensued, and each lizard consumed its own half. That such competition has some effect was shown by the fact that on another occasion a lizard seized one of the larvae and, on putting it out, another lizard came to inspect it. The first lizard immediately picked up the larva again and ran away with it. It subsequently put it out again. Though it could not eat it, it would not give it up to the other.

Having satisfactorily proved the distastefulness of the insect, it occurred to me to try the effect of a change of food plant. Several larvae were placed upon apple leaves, which they readily consumed. After this diet had been continued for a few days, the caterpillars were again presented to the lizards, when they ate them without the slightest hesitation. Though the experiment was repeated again and again, on no single occasion was an apple-fed larva refused after being once tasted. This experiment, while discovering a case similar to that of *M. typica*, above described, also showed that if a larva were capable of changing its food plant, it might also undergo a great change in its edible qualities. An interesting light is thus thrown on a peculiar natural development. An insect which had hitherto escaped its enemies by its cryptic habits and coloration might be ultimately sought out by its foes, and if the latter were sufficiently numerous and persistent, they might cause its extermination. Some few might, however, survive for the time being on another food plant which unexpectedly gives them nauseous qualities; and, as in the case of *M. typica*, makes possible the development of conspicuous colours, and what was once an edible cryptic larva might thus quite conceivably become a warningly-coloured distasteful species. At least the supposed difficulties of those first stages in the development of distastefulness are, in the light of these results, further considerably minimized, since, other factors being equal, the slightest variation towards conspicuousness would now assist the larva in the struggle for life. The question may very properly be asked whether the moths resulting from ivy-fed larvae are distasteful, and those from apple-fed larvae palatable. This question I am as yet unable to decide, but though deeply interesting the reply would not greatly affect the argument, since distasteful qualities must arise first in the larva, and that is the only stage in which their origin presents a difficulty.¹

We may now proceed to consider experiments which have been made abroad with a view to testing the degree of edibility of butterflies and other insects. M. de Nicéville experimented with a common species of mantis and found that whilst it ate most of the butterflies which he gave it, it always refused *Acraea violae*. Mr. Frank Finn, Deputy Superintendent of the Indian Museum, made numerous experiments in 1895, 1896, and 1897, with Indian birds and lizards, by feeding them with butterflies. The results of these experiments showed that while the lizards did not show very much discrimination, the birds, though in many cases eating the distasteful kinds, showed on the whole a good deal of preference for the non-warningly coloured species. At the conclusion of the account of his 1895 experiments Mr. Finn says, 'these experiments left not the slightest doubt in my mind as to the unpalatability of *Danaïs* and the other "warningly-coloured" forms. Birds would often only look at them, and soon left them when picked up' (Journ. Asiatic Soc. of Bengal).

¹ Since the above was written three of the moths have been hatched out and presented to lizards and a bird (*Graculifera melanoptera*). The insects were eaten without any signs of distaste. Though such a

small number of moths were available it seems reasonable to suppose that the distastefulness of the larva is not continued in the imago. The moths are extremely cryptic and resemble leaves.

The same experimenter found that while *Delias eucharis* was one of the most distasteful of all butterflies to many species of Indian birds,¹ in East Africa the moth *Egybolis vaillantina* was refused by a chameleon and a gecko.² Colonel Yerbury, on the other hand, observed a mantis at Trincomali hanging from a flower and capturing the butterflies which were attracted by it. He saw it eat *Delias eucharis* on several occasions.³ Mr. F. Muir found that *D. chrysippus* was rejected by a mantis at Mozambique even when hungry.

The most extensive and valuable experiments made in connexion with the bionomics of butterflies and other insects are those which were carried out by G. A. K. Marshall in South Africa. The results, together with most interesting and comprehensive comments thereon, were published in a joint paper by Mr. Marshall and Professor Poulton and communicated to the Entomological Society in 1902.⁴ This memoir occupies some 300 pages of the Transactions, and is illustrated by fifteen plates. It is difficult to exaggerate the importance of this paper, and to express the great indebtedness of students of mimicry to the authors. To Mr. Marshall for his patience and conscientiousness in carrying on the work, and to Professor Poulton for his valuable comments on the results attained. It should be taken as a 'model for mimicry' by all those who have the opportunity of making such experiments, since the value of personal observations of this kind can hardly be over-estimated. Mr. Marshall's experiments cover a very wide field of research, and include the account of his well-known discovery with reference to the seasonal forms of *Precis*, together with copious notes on a great variety of interesting observations. The value of the work is greatly enhanced by numerous discussions on the results of the experiments and on subjects suggested by them.

Mr. Marshall first investigated the butterfly-eating capacity of various species of mantis. The distastefulness of *Acraea horta*, even for a mantis, was shown by the fact that the insect 'ran towards it, and seized it and made a bite at the back of the thorax, but started back as if in great surprise, and wiped his mouth on his front legs'. On another occasion the same mantis 'tackled it at once, seizing it from above and biting the thorax, but he quickly let go and began wiping his mouth as before. A few minutes later he made a second attempt with the same result'. Later on the *Acraea* was again placed close to the mantis, when he began to eat it, but soon threw it down again, and would not touch it although no other food was given for twenty-four hours. On another occasion a mantis, starved for twenty-four hours, ate *D. chrysippus* all except the limbs. A third *A. horta* was caught and bitten by the mantis, but it 'started back with disgust just as in the previous experiment, but his efforts to get rid of the nasty taste were more prolonged. For over five minutes he continued cleaning his mouth on his fore-legs, or rubbing it from side to side on the gauze.' Another mantis was given *Acraea serena*, but after biting it threw it down and ejected a brownish liquid from its mouth, and also wiped its mouth with its legs. On another occasion *Acraea natalica* was given, but after being bitten was dropped at once; a second attempt was made and the butterfly again dropped. *Acraea serena* was also rejected. The mantis readily consumed other butterflies, including *D. chrysippus*, *Charaxes varanes*, *Papilio demodocus*, *Neptis agatha*, *Pyrameis cardui*, and many others. The same insect died after eating two *chrysippus* and one *cabira*, but whether as a direct cause cannot be certainly concluded. Another species of mantis (*Pseudocreobotra walberghi*) after an exclusively *Acraeinae* diet, became paralysed in the mandibles and partially blind. The

¹ Journ. As. Soc. Bengal, 1897, p. 667.

² 'Natural Science,' 1892, p. 747.

³ Trans. Ent. Soc., 1902, p. 316.

⁴ 'Five Years' Observations and Experiments on the Bionomics of S. African Insects,' Marshall and Poulton, Trans. Ent. Soc., 1902.

same result followed with 'a Charaxes-eating mantis' fed principally on *Acraeas* for about eleven days. This mantis evidently only ate the *Acraeas* with considerable compunction. Another mantis of the same species was fed on *Acraeas*, and though it showed great dislike of *encedon* and *serena*, and absolutely refused to eat *Pardopsis punctatissima*, one of which was caught and rejected no less than seven times, the insect did not, at the end of about a fortnight, exhibit signs of ill health. This experiment was not continued.

A large green mantis (*Sphodromantis lineola*) was fed on *Acraeas* for about three weeks. It tasted and constantly rejected *caldarena* and *halali*, but during the period ate about nine *Acraeas*, mostly *caldarena*, after which it became partially blind and died.

Another mantis of the same species was fed on butterflies for over a fortnight. The species did not include any *Acraeas*, but were of such genera as *Junonia*, *Precis*, *Terias*, *Catopsilia*, &c. The mantis consumed them all eagerly, and during the period named devoured thirty-six examples. It escaped from its cage and was fully as vigorous and healthy on the last day as when first caught. Another mantis, which it was thought might be a seasonal form of one of the others experimented with, ate many *Acraeas* and *Danaines* from April 3 to September 8, when it died. It did not show the same signs of distaste so evident in the other examples, though it would not eat *Acraea axina*. It did not become blind or show marked signs of ill health.

The same investigator then proceeded to experiment with spiders, the species made use of being *Nephilengys malabarensis*. These tests had the advantage that the spiders were not in captivity, as were the mantises. The following is a summary of the results, the number corresponding to the observations made.

1, 2, and 3. *Acraea horta* was eaten only when the wings were cut off, entire specimens being immediately rejected.

4. Wingless specimens of *D. chrysippus* were at once thrown out of the web.

5. Wingless specimens of *P. brasidas*, *P. ophidicephalus*, *P. euphranor*, *E. hiarbas*, and *P. lyaeus* were all promptly eaten.

6. *Acraea horta* with the colour rubbed off was wrapped up and carried off.

7. The same species was ejected after being bitten, and subsequently after the colour had been rubbed off, and again after the wings were cut off.

8. Wingless specimens of *P. demodocus* were eaten.

9. *Acraea horta*, after being several times bitten, was eventually carried off, but ultimately thrown away.

10. Unsucked specimens of *A. horta* were observed in spiders' webs in the bush.

11. Three wingless specimens of the same species were rejected, but one was sucked by another spider.

12. A wingless *Amauris echeria* was rejected by four spiders, two of which bit it and then would have nothing to do with it.

13. *Terias brigitta*, *Nepheronia argia*, and *Precis sesamus* were readily eaten.

14. *A. horta* was again refused after tasting.

15. *A. violarum* was refused by three spiders.

16. *A. horta* was ejected from the web by two spiders, tasted and rejected by a third, and ignored by a fourth.

17. *A. buxtoni* and *Nepheronia argia* were eaten.

18. *P. hellica*, *P. demodocus*, and *Acraea esebria* were eaten, the last with suspicion.

19. *Byblia goetzius-acheloia* was eaten after a time.

20. Wingless specimens of *A. horta* promptly ejected by three spiders, but a fourth

wrapped hers up and carried it off. She turned it over several times, bit it here and there, and then left it, ultimately throwing it away.

21. *A. serena-buxtoni* was eaten by three spiders. It is to be noted that this species exudes a bitter yellow juice when captured, and thus may have lost much of its nauseous qualities and would be less distasteful than if caught by the spiders direct.

The author draws very interesting conclusions from the experiments. He points out that invertebrate enemies such as spiders and mantises do not appear to appreciate warning colours, and that herein, no doubt, lies the great advantage to the victims, of the great tenacity of life in distasteful insects. Inedible qualities alone would not protect an insect against experimental tasting by enemies which did not recognize its aposematic coloration, whilst tenacity of life in edible forms would be of no assistance, since they would very seldom escape after being caught and tasted. The great tenacity of life possessed by distasteful butterflies such as *Acraeinae*, and *Danainae* has been frequently noticed by collectors, as instanced by Trimen's remarks already quoted. The usual nip under the thorax does not kill them, whilst the wings may often be bent almost double without any apparent injury, so supple are the nervures and membranes.

Marshall's experiments with lizards and frogs gave but little result, as the lizards obtained did not appear to be species which habitually fed on butterflies, and also they did not thrive in captivity. That lizards do, however, prey on butterflies is shown by the fact that he frequently observed these animals stalking butterflies at rest 'with much astuteness', and in another passage, speaking of *Precis sesamus f. natalensis*, he says, 'It is very wary and difficult of approach, being kept on the alert by its enemies the lizards. I have often watched these little reptiles stalking both *natalensis* and *pelasgis* round the stones, and have seen them capture and eat both species.'

With birds more success was obtained. A young kestrel, after tasting an *Acraea caldarena*, threw it away and would eat neither it nor other *Acraeas* which were offered, though it ate with relish *Precis pelasgis*, *Junonia cebrene*, *Precis sesamus*, and *Atella phalantha*. Another of these birds, though of a different species, refused *A. halali*, *A. anemosa*, and *L. chrysippus*, shortly afterwards eating *B. ilithya* and *Terias brigitta*. Under stress of hunger this bird ate part of an *A. caldarena*, but threw away the rest. On another occasion the same bird, after eating some other butterflies, was offered *D. chrysippus*. After one or two pecks it was thrown away. The bird then ate *H. daedalus* and tasted *A. caldarena*, which it threw away after eating a small part; *P. sesamus*, *J. cebrene*, and *B. ilithya* were then eaten with relish. After being starved for twenty-four hours, this bird ate ten butterflies and several grasshoppers. Amongst the former were *A. caldarena*, *A. rahira*, *A. axina*, and *A. halali*. One *D. chrysippus* was partly eaten, and one was refused. These tests afford good evidence of the distastefulness of *Acraeas*, and also point to the conclusion that *D. chrysippus* is, to birds at any rate, still more objectionable.

A tame ground horn-bill (*Bucorax caffer*) ate three *A. serena*, one *P. lyaeus*, and one *H. misippus*, but immediately dropped *D. chrysippus* after crushing the thorax, and shortly afterwards treated a second example of this butterfly in the same manner. On other occasions this bird ate eighteen butterflies, including five *Acraeas*, and again six butterflies including four *Acraeas*. *Acraeas* were apparently not particularly objectionable to this bird, though it is significant that it would not eat *D. chrysippus*, the conclusion being that the latter was very much more distasteful, whilst it will be remembered that one of the mantises did not appear to make any distinction.

A very young female mongoose (*Herpestes galera*) was experimented upon with insect

food, and though the experiments were not numerous some of the results are very significant. Thus the author says, 'I then gave her four *T. senegalensis* without wings, which she ate greedily, and on being offered a *Mylothris agathina*, she promptly seized it, but immediately jumped back so violently that she rolled head over heels. The way she shook her head clearly demonstrated the distastefulness of the butterfly, and she would not let me bring it anywhere near her. I then offered her a *Belenois mesentina*, but with the same result; she refused to touch it every time. Thinking this might be due to her experience with the *Mylothris*, I put the *Belenois* aside and offered it to her ten minutes later, when it was eaten with undoubted relish. An *Acraea caldarena* and *A. axina* were then refused, but without being tasted, the smell being apparently quite sufficient.' This animal varied considerably from time to time in its likes and dislikes, for Mr. Marshall tells us that about a week after the above tests *Mylothris agathina* was eaten and the following day two more of the same species without apparent distaste. Three days later it ate three *A. axina* and one *D. chrysippus*, although a few days after this it refused both *chrysippus* and *axina* 'with unmistakable signs of distaste'. The results are somewhat contradictory, though the animal quite evidently disliked *chrysippus* and *axina* after previously eating them. The next experiments described were with a monkey (*Cercopithecus pygerythrus*). This animal ate with great caution, a *Precis sesamus*, and afterwards readily devoured *P. pelasgis*, *sesamus*, *B. acheloia*, and two *P. antilope*. It then took *Acraea halali* and put it into its mouth, but quickly taking it out again looked at it 'with the utmost surprise for some seconds', and then threw it away. After this the monkey would have nothing to do with an *A. caldarena*.

Mr. Marshall next describes experiments made with captive baboons. These animals being capable of considerable facial expression, it would naturally be expected that interesting results would be obtained, and such indeed proved to be the case. Insects other than Lepidoptera were offered, as was the case in some of the previous experiments, and striking proof of the theory of warning colours was obtained. The following tests were made with butterflies. A young baboon ate *Belenois severina* and *B. mesentina* with evident relish, also *Colias electra* and *B. ilithya*. It tasted and rejected *A. caldarena* and *D. chrysippus*, and rejected at sight several *A. axina* and *A. halali*. Two *D. chrysippus* and one *A. anemosa* were refused at sight, *Neptis agatha* was tasted and neglected, whilst *B. severina* and *Teracolus achine* were eaten. A very significant result must here be given in the author's own words. 'A *Mylothris agathina* was taken with some doubt, the head and thorax were eaten, and a small part of the abdomen, the rest being thrown away; it was clearly not much appreciated. A *D. chrysippus* was tasted and refused. Then an *Acraea anemosa* was offered with underside exposed to show the bright red and black markings; it was tasted and refused. A *Precis sesamus* (wet season form) was then offered in precisely the same manner; the baboon took it, held it in her hand for a few moments, and then let it fly away without attempting to smell or taste it. I then cut the wings off another specimen of the same insect, and this was promptly eaten without any signs of distaste.' The significance of this passage cannot be overlooked. The baboon, having found *anemosa* distasteful, clearly associated its experience with the colour of the insect, and thus the *Precis*, though only bearing a very rough resemblance was allowed to escape, in spite of its edibility, which was immediately afterwards proved. No more convincing demonstration of the working of the principle of Batesian mimicry could well be conceived.

Further experiments with other insects then followed, the most remarkable result being the evident relish with which the baboons ate certain large and evil-smelling bugs, showing the unreliability of human senses in regard to insect flavours. An attempt was made to estimate

the value of the somewhat Acraeine appearance of *Byblia ilithya* by offering them with the underside exposed. They were eaten with evident appreciation. *Acraea rahira* was then offered in the same manner, but the animal recognized it and threw it down without even smelling it. Two more *ilithya* were then eaten, and an *A. axina* and *B. ilithya*, being offered together, the animal ate the latter and neglected the former. The baboon was clearly able to distinguish between these two butterflies by their pattern. Some doubt about *ilithya* was, however, shown on a later occasion, when the baboon pulled one to pieces and threw it down, then, changing its mind, picked up the thorax and ate it, immediately afterwards eating three more specimens in quick succession. On another occasion *Precis archesia*, two male *H. misippus*, two *B. ilithya*, three *A. phalantha*, and one *P. sesamus* (wet form) were eaten, whilst *M. agathina*, *A. natalica*, and *P. sesamus* (dry form), were refused. *M. agathina* was subsequently eaten with reluctance, and a second example was refused after tasting. *Neptis agatha* was treated in the same way, but two *B. severina* were eaten with relish. *P. sesamus* and *H. misippus f. inaria* were readily eaten. Two large *Hesperidae* were eaten 'with avidity' and the baboon watched with great eagerness the opening of another box, being obviously disappointed on receiving *B. mesentina*, which, however, was eaten. *Herpaenia eriphia*, after being carefully tasted, was rejected. As showing the comparative distastefulness of *M. agathina*, Mr. Marshall describes how the baboon seized that insect and *B. mesentina*, and began eating them both at once. It then put them out and picked up the *Mylothris*, tasted it and threw it away, afterwards eating the *Belenois*. The other baboon picked up the *Mylothris*, but after tasting it also at once threw it away.

These results are amongst the most interesting and conclusive yet recorded, and it is greatly to be desired that further experiments will one day be made. In view of what has been described we can no longer entertain the slightest doubt that many butterflies are in fact nauseous to insect-eating animals, whilst others are obviously much relished. That tastes differ somewhat is also shown by the difference in the behaviour of insects, reptiles, birds, and mammals, and this is what we should naturally expect, since it is manifest that even generally unpalatable species cannot be protected from all their foes, otherwise they would multiply indefinitely. Since some species are undoubtedly protected by their distastefulness, the theory of mimicry must stand on a sound basis, as, given this one fact, it follows that outward resemblance to such protected kinds must of necessity be an advantage to an edible species, and this conclusion is not in the least affected by any arguments as to the manner in which such resemblance may have been brought about. Endeavours have been made to show that insects which are distasteful to their enemies are not possessed of any nauseous qualities whatever, since certain naturalists have, albeit with most praiseworthy devotion to science, overcome their natural disinclinations, and actually tasted butterflies and moths. Professor Felix Plateau¹ tasted the larva, pupa, and imago of the Magpie moth, so persistently refused by birds. He describes the larva as devoid of any unpleasant flavour, in fact rather agreeable than otherwise, and somewhat recalling that of sweet almonds or cocoanut. The pupa and imago produced a similar impression, though to a feebler extent. Professor W. M. Wheeler, of Texas University, also tasted some conspicuous day-flying moths (*Pseudobasis*) with precisely similar results.² Mr. Marshall himself made some tasting experiments on African butterflies.³ He describes *A. encedon* as exuding a slightly bitter juice from the thorax. *A. anacreon* and *natalica* a similar juice, but 'distinctly more bitter', whilst *A. anemosa* emits both the bitter juice and a very strong smell.

¹ See Mém. de la Soc. Zool. de France, 1894, p. 375 (quoted by Poulton, Trans. Ent. Soc., 1902, p. 405).

² 'Century Magazine,' 1901, p. 378 (also quoted by Poulton).

³ Trans. Ent. Soc., 1902, p. 413.

Planema aganice emits an acrid juice and *A. echeria* and *Alaena amazoula* are described as having a nauseous taste and a strong smell. *A. horta* emits a bitter juice, but *D. chrysippus* did not appear to have any taste at all, nor was any smell noticeable. In this latter respect it is interesting to recall the evidence of Drs. Dixey and Longstaff, who both perceived a strong odour about this butterfly. As pointed out by Professor Poulton in describing these experiments, such tests are, and probably always will be, quite unsatisfactory and inconclusive. We cannot judge of the perceptions of insectivorous animals, or even assume that there is any comparison to be drawn between their sensations and our own. The fact that they refuse to eat certain insects whilst others are greedily devoured, is really all that concerns us. It may be added that what we call taste, and especially the refinement of taste expressed by the term flavour, is largely a matter of the olfactory sense. Now the sense of smell is well known to be but poorly developed in human beings. The power of scent in many animals is developed in a manner which we can but feebly comprehend, and hence the sense of taste must be very greatly modified. Thus we see the baboons very clearly distinguishing between *M. agathina* and *B. mesentina* with a delicacy of perception of which we can have little real comprehension. We may compare in this connexion the words of the late Sir Michael Foster,¹ 'The sense of smell seems to play a far more important part in the lives of the lower animals than it does in our life; and what we now possess is probably the mere remnant of a once powerful mechanism. We may perhaps connect with this, on the one hand, the fact that, even in ourselves, the olfactory fibres have allotted to them what is virtually a whole segment of the brain, namely, the olfactory lobe, and, on the other hand, the fact that olfactory sensations seem to have an unusually direct path to the inner working of the central nervous system. Mental associations cluster more strongly round sensations of smell than round almost any other impressions we receive from without, and powerful reflex effects are very frequent, many people fainting in consequence of the contact of a few odorous particles with their olfactory cells.' These words are full of meaning for our present subject. We can see how it may be probable that on the ultra-sensitive olfactory organs of many animals 'flavours' of which we are quite ignorant may have an effect both powerful and lasting, and thus the possession by an insect of properties which produce these sensations in their enemies may well turn the delicately adjusted balance of nature in their favour. The experiments which have been described above can leave no doubt in our minds that insects do in some cases actually possess such properties. It matters little whether we call them taste or smell. If the existence of the objectionable character can be associated in the mind of the captor with the appearance of the insect, as indeed the behaviour of the baboons shows to be actually the case, then it requires very little argument to maintain that the development, however evolved, of an imitative appearance in an edible species, must of necessity confer on its possessor some share of whatever degree of immunity the objectionable species may enjoy.

It is greatly to be hoped that others whose work takes them to tropical lands, and who are sufficiently interested in these subjects, will undertake further experiments on the lines of Marshall's splendid work. The unexpected so frequently happens, when practical tests are made, that even the amateur need not hesitate to add to our existing store of knowledge whatever results he may be able to obtain. Meanwhile it seems unnecessary to further argue the broad question of the comparative inedibility of many insects. No unbiassed reader could remain long in doubt after studying even the comparatively small amount of work which has already been accomplished in this connexion.

¹ 'Textbook of Physiology,' Part iv, p. 1390.

IV

ON THE EVIDENCE THAT BUTTERFLIES ARE PREYED UPON BY BIRDS

As already noticed, the supposed lack of evidence that birds do in fact exercise a great selective influence on butterflies has always been a strong point in the arguments of those who find a difficulty in accepting the view that mimetic resemblances are produced by natural selection, and it must be admitted that for some time after these problems began to occupy the attention of naturalists the direct evidence in support of the assumption was by no means plentiful. It was argued that if birds are so powerful a selective force the destruction of butterflies by them should be a matter of everyday occurrence, easily observed and accepted without question. A little consideration, however, will show that the subject is by no means so simply and easily dismissed. Are we, as a matter of fact, so very familiar with the details of the everyday life of the wild creatures which surround us? In temperate regions the diversity of forms of animal life is not developed to anything like the extent which is attained in the tropics. Our sharply-defined seasons materially reduce the opportunity for the rapid reproduction which takes place in regions nearer the equator; and thus we find that the methods of deception employed by various forms to ensure the survival of their species are much less numerous and diverse than is the case in tropical lands. There we find life manifested in swarming hosts of creatures amongst which the competition for existence is such that only those which have evolved a very perfect adaptation to their surroundings remain as evidence of the struggle. In our own country we have ample opportunity for studying the habits of our native animals, and yet if the question arises as to whether certain birds are, from an economic point of view, destructive or beneficial, large numbers must be shot and their crops examined before anything can be definitely stated as to their habitual food. If we examine the statements of the opponents of the selective theory, it is found that the evidence is largely of a negative character. That birds are not commonly seen to eat butterflies may be a fact, but this is not good evidence that they seldom or never do so, and thus we come to one of the strongest arguments against the kind of negative assumption so frequently proffered, an argument used by Marshall in his paper on 'Birds as a Factor in the Production of Mimetic Resemblances in Butterflies',¹ which is that, from those who maintain that birds do not eat butterflies, we are justified in demanding a list of the insects which birds *have* been seen to eat. Before I was aware that Mr. Marshall was making a special study of this subject, I had begun, for the purpose of the present memoir, to collect instances of birds preying on butterflies. My own work in that direction had not, however, proceeded very far when the above-mentioned paper appeared. Needless to say, the work has been carried out with a completeness which I could not have hoped to attain, and as the author, with characteristic generosity, at once placed the paper at my disposal for the present purpose, it must be understood that I am indebted to him for the information here furnished. In the face of the many assurances given from time to time by

¹ Trans. Ent. Soc. 1909, p. 329 et seq.

collectors that they have never observed the destruction of butterflies by birds, it is refreshing to find a frank expression of opinion to the contrary, and here we find Dr. Franz Doflein, who has a large experience, expressing his surprise that naturalists who have had collecting opportunities in the tropics should have failed to observe what he himself evidently regards as a common occurrence. Instancing the facility with which such facts may be overlooked, Marshall points out how rarely ornithological works mention facts of this kind, and yet Parkinson Curtis, as recorded in 'The Entomologist' of 1903, records that a kestrel observed on Ballard Down, near Swanage, was continually swooping down and catching and eating butterflies on the ground. In the course of an hour some thirty-six specimens were captured in this manner, whilst the bird was observed to continue the pursuit for at least five hours. Here a single bird in one day may reasonably be assumed to have destroyed 180 butterflies. and as the observation was confirmed in succeeding seasons by Mr. Curtis, and independently by Mr. Colthrup, it is evident, as the author indicates, that butterflies are a common food of the kestrel, and yet its habit in this respect has been quite overlooked. The garden warbler is further instanced by Professor Kennel as having been observed by him to feed its young 'almost exclusively on butterflies all day long'. Further instances of a similar kind are adduced, showing that absence of direct evidence for the fact is by no means necessarily evidence against it. A long list of instances is then given of attacks on butterflies in the Palearctic region. No less than thirty-four species of birds are recorded on seventy-eight occasions as having been seen to feed on butterflies, and thirty-eight species of the latter were observed to have been attacked. As an instance of the kind of statement made by the opponents of mimetic theories, Marshall quotes the remark of H. P. R. in 'Country Life', March 14, 1908, p. 384, which reads as follows: 'No one has been able to adduce any examples of a bird eating a butterfly, beyond a few cases where the food was either the Meadow Brown or the Large Heath (*E. janira* or *E. tithonus*), or the Green Hairstreak—out of thousands of observers, entomologists and ornithologists.' The mass of evidence in the Palearctic region alone is a sufficient reply to this surprisingly confident and inaccurate statement. It may be added that out of the seventy-eight occasions above referred to, these three butterflies were observed to constitute the prey in only six instances. In tropical regions the available records are naturally fewer, not because such attacks are of less frequent occurrence—they are undoubtedly much more common, but because the number of naturalists who have had an opportunity of recording such facts is comparatively small. Nevertheless, in Africa, thirty-one species of birds, together with certain cases where the bird was not identified, are recorded as having attacked thirty-one species of butterflies on forty-five occasions. It is worthy of note that, even in this comparatively small number of observations, the protected nature of certain dominant forms is evident. There are only four attacks on species of the genus *Acraea* and none at all on Danaine butterflies, further proof, if any were needed, of the distastefulness of these groups.

Out of nine recorded attacks on *Nymphalinae* only two are in connexion with a species having a mimetic association, and these are both *Atella phalantha*, which is synaposematically associated with *Pseudargynnis hegemone*. Out of the five recorded attacks on species of the genus *Papilio* none of these were mimetic, though one was the male of *dardanus cenea*. These facts should be borne in mind, since it has been stated by those who deny the value of warning colours, that when birds have been seen to attack butterflies they attack the so-called protected species as frequently as any others. The records of attack in the Indo-Malayan region are equally instructive. Thirty-one identified and eight unidentified species of birds have been seen to attack fifty-one species of butterflies on seventy occasions. Of

these there were only four instances of attacks on *Danainae*, and in these two of the species were refused, one, (*T. septentrionis*) after inspection, and the other (*Danaida* sp.) after tasting. Only once was an *Acraea* seen to be attacked and eaten. In the Nearctic region forty-six identified species of birds, and many unidentified, were either seen to attack butterflies or were found on dissection to have eaten butterflies, of which some twenty-six species were identified. Here again it is a remarkable fact that on the only occasion when the common Danaine, *Anosia plexippus*, was seen to be attacked, the insect was immediately dropped again without being eaten.

The records from the Neotropical region are extremely few, and yet, judging from the extent to which butterfly mimicry has been developed in the South American species, such attacks must be of frequent occurrence. One instance, however, is very instructive. It is the statement of Pöppig, given by Haase in his 'Researches on Mimicry', that 'there is no difficulty in recognizing the favourite perch of a *Galbula*, for the wings of the largest and most splendid butterflies, whose bodies alone are eaten, cover the ground for some steps around'. It may safely be assumed that such an observation, though proving that 'the largest and most splendid butterflies' are eaten, does not preclude the destruction of other and smaller species, since the wings of these would be less easily observed. Many of the observed instances of the attacks of birds on butterflies are of special interest. Thus in Africa, Swynnerton records that a White Spotted Flycatcher (*Trochocercus albonotatus*) darted out at a *Mylothris*, but turned back on reaching it without an attempt at capture. Most of the forms of *Mylothris* serve as models for other species, and we are justified in concluding that the bird in this case recognized a distasteful species. In other instances given by Captain Boyd Alexander, a Bee-Eater which he shot had its mouth 'so stuffed with butterflies that it appeared to me marvellous that it had not choked'. Again, in the Indo-Malayan region, it is recorded by Sir George Hampson (Proc. Ent. Soc., 1897, p. xxxviii), that in the cases which he had seen of birds attacking butterflies the *Euploeae* and *Danainae* were attacked as often as any others, 'but usually escaped eventually from the beak of the bird, and flew away none the worse, owing to the toughness of their integuments.' This statement, which was made rather with the intention of discounting the mimetic theory, certainly strengthens it. It is not the habit of animals in a state of nature to allow their prey when once captured to escape, and if the *Euploeae* and *Danainae* do thus avoid destruction, it must be on account of qualities which convey unpleasant sensations to their enemies. E. L. Arnold, in 'On the Indian Hills', describes the ground beneath the 'watch towers' of the Green Bee-Eater as being 'thickly strewn with gaily painted shreds of unfortunate butterflies and bees'. Now whilst it is the habit of these birds to eat butterflies they are evidently not always specially adapted to eat distasteful species, since E. H. Aitken (Journ. Bombay Soc., xvi, 1904, p. 156) records that a Bee-Eater 'caught a *Danaïs*, but dropped it as soon as it had tasted it, and the *Danaïs* flew away little the worse'. Lieut.-Col. Bingham (Trans. Ent. Soc., 1902, p. 362) records that Bee-Eaters habitually attacked many species of butterflies, but that he particularly noticed that they never went for a *Danaïs* or a *Euploea*, or for *P. macareus* and *P. xenocles*, which are mimics of *Danaïs*, though two or three species of *Danaïs*, four or five of *Euploea*, and the two above mentioned mimicking *Papilios* simply swarmed along the whole road.

Apart from the direct evidence afforded by the numerous instances in Marshall's paper, there is in the Hope Museum at Oxford a large collection of butterflies, which have been injured by the attacks of insectivorous animals, principally birds and lizards. Very many of these have been seized when at rest, as is shown by the perfectly symmetrical injuries, taking the form of notches in opposite wings which exactly coincide when the wings are closed. Some eighty-two such specimens are illustrated on Plates IX, X, and XI, in Trans. Ent. Soc., 1902, and the descriptions of the plates give notes on each species, and the probable

enemy which caused the injury. The illustrations form part of Marshall and Poulton's extensive paper on the bionomics of South African insects already referred to. I have here endeavoured to give a condensed account of the large number of instances which have been collected bearing on the present subject. No one who has studied Marshall's paper could remain longer in doubt that birds are potent factors in the selective forces which guide and control the evolution of butterflies. Their attacks are not exceptional phenomena, but matters of habit and everyday occurrence. The manner in which such observation may for long go unobserved is instanced by the case of the kestrel, which is now known to habitually eat butterflies. If cases of this kind can remain so long unobserved in our own country, where every wild creature has been carefully studied, it would indeed be rash to assert that birds in tropical lands do not attack butterflies. It will probably be admitted that we are not even acquainted with all the species of birds which inhabit the tropics, and our knowledge of the economy of those species which have been described cannot yet be so perfect as to enable any one to decide definitely as to their choice of prey. To sum up the whole matter, there is on the one hand no sort of proof that birds do not exercise a selective influence on butterflies, and hence that they 'have been but little concerned in the matter',¹ whilst on the other hand, where evidence to the contrary has been sought it has been found in plenty, not only in reference to the preliminary contention, but still further in direct confirmation of the hypothesis that some butterflies are less liable to attack than are others. The mainstay of the argument of those who see so much weakness in the mimetic theory suffers from the very form of instability which they allege in the contentions of its supporters—it is based largely on assumption.

As regards any early instinctive knowledge in birds of what to eat and what to avoid there can be but little doubt that young birds learn only by experience to make a choice of food. Those who have read Lloyd Morgan's work on 'Habit and Instinct' will remember that his young birds at first struck at anything of suitable size, whether eatable or not. The list of objects which the author gives as forming their early prey includes chopped wax matches, bits of paper, buttons, beads, cigarette ash, their own toes and those of their companions, specks on the floor, and, in short, 'anything and everything, not too large, that can or cannot be seized is pecked at and, if possible, tested in the bill.' It is pointed out that there seems to be no congenital discrimination between nutritious and innutritious objects, or between those which are nice and those which are nasty. The larvae of the Cinnabar moth were tested and rejected, and the birds, after being fed with other larvae, still remembered the former and refused them. Similarly, moorhen chicks soon discriminated between small edible beetles and 'soldier beetles', though, as the writer states, 'such discrimination is not congenital, but acquired.' Again, in another passage, 'My observations with regard to the effects of giving to young birds distasteful insects were made solely with a view to ascertain whether there was any instinctive avoidance on the part of the birds. Of this I have not found a single instance.' The author is careful to point out that there may be such instinctive avoidance in young birds which, when hatched, are devoid of parental guidance, since 'such guidance would in some degree prevent the incidence of natural selection, and would diminish the elimination of those which without such guidance might eat to their destruction'.² Much more information on the same points is to be found in the work in question, which I commend to the study of those interested in these matters. For the present purpose it suffices to call attention to the fact that experimental proof is not wanting in regard to the necessity of young birds learning what to eat and what to avoid.

¹ Quoted from Dr. Sharp's remarks on mimicry in 'The Cambridge Natural History'.

² It is not however intended by supporters of the mimetic theories that distasteful insects are also poisonous.

GENERAL CONCLUSIONS

FROM the evidence adduced in the foregoing sections it may fairly be claimed that the two main contentions are not without substance in fact. There are dominant groups of butterflies, many of them are distasteful, some possess this quality in a high degree. Moreover, it is evident that butterflies do form the prey of birds and other insectivorous enemies. It will probably not be questioned that an animal having gustatory preferences will choose the most palatable food, and hence it follows that if a palatable butterfly so closely resembles another which is distasteful it will have a superior chance of escape by reason of its resemblance. It seems unreasonable to abandon a theory based on natural selection unless the alternative can be shown to explain some features of the phenomenon which are otherwise inexplicable.¹

If butterflies have come to resemble each other by the operation of similar environmental causes, then mimicry between these insects must be something apart from other forms of mimetic resemblance, since environment can hardly be suggested as a cause of the resemblance of an insect to a dead leaf, nor would sexual selection be of any avail. Moreover, the appearance of a butterfly or other insect having a complete metamorphosis is provided for in its larval and pupal stages, since the pattern of the perfect insect is complete at the moment of emergence. It may be said that in the larval state there is every scope for the production of similar effects by local causes. To go no further, however, than the order Lepidoptera, it would be difficult indeed to imagine how any force of environment could account for the case of *Papilio laglazei*,² and its model, *Alcidis aurora*. The supposed external causes which have acted on the two insects have produced a real orange-coloured body in the moth and an imitation one in the butterfly. The only uniformity of result which has been produced is the very deceptive one of appearance, brought about by methods widely different in their nature. Turning to certain resemblances in Neotropical Lepidoptera, we have the mimicry between forms of *Castnia* and Ithomiine butterflies, as instanced by Professor Poulton. Here the larvae of the former feed inside the stems of plants, whilst those of the latter

¹ The argument in favour of natural selection will be found in a paper by Professor Poulton, entitled 'Natural Selection the Cause of Mimetic Resemblance and Common Warning Colours', and published in the Linnaean Society's Journal (Zoology), vol. xxvi, p. 558, &c., and a revised edition is included in the collection of 'Essays on Evolution' by the same author. The subject has been so fully and ably dealt with in these publications that I feel I can add

nothing of importance to the convincing evidences there adduced. In fact, had it not been necessary, for the completeness of the present work, to make use of some of these arguments I should have been inclined to avoid the subject, since I can at best but call attention to truths which have been expounded by a far abler pen than mine.

² See p. 41.

feed openly on the leaves of the food plant. The larval environment is quite different, and yet the resemblance between the perfect insects is extremely close. Difficult as these cases are under a theory of external causes, they are as nothing to cases of mimicry between different orders of insects, where there is no such thing as even approximate similarity of environment in the larval stages, since many of the flies which so closely imitate Hymenoptera subsist in their early stages on putrefying organic matter. In view of the frequency with which sexually dimorphic mimicry is developed, any theory based on the influence of environment must presuppose that such influence acts differentially on the two sexes. The case of *P. eurytus* and *P. epaea* would comply with such a view, were it not that we are at once faced with the difficulty that both sexes of *E. phegea* mimic the female *P. epaea*. Again, in West Africa the female of the sexually dimorphic *Mimacraea fulvaria* mimics the male of *Acraea alciope*. If external causes produce mimicry they must either affect both sexes alike or at least they must affect similar sexes. The above instances show that they do neither. As has been pointed out in an earlier portion of the work, the resemblance between certain Neotropical butterflies is brought about by the transparency of their wings. This transparency has been shown to be produced in a great variety of ways. If external or internal causes can produce resemblance, then those causes must be uniform and must produce their effect by uniform means. The mimicry of these transparent butterflies is evidently not produced by such influences. Finally, it is a coincidence of more than ordinary peculiarity that these supposed all-powerful environmental influences should exert their forces only to produce such resemblances as will cause their possessors to be mistaken for creatures which are nauseous to the palates of their enemies, or which possess stings or other offensive or defensive attributes.

It is to be observed that few of those who find a difficulty in accepting existing theories concerning the mimicry of one butterfly by another, experience any difficulty in recognizing the numerous other forms of mimetic resemblance which are found in nature—the resemblance of butterflies to leaves, of caterpillars to twigs, of harmless insects to those of other orders protected by defensive qualities. And yet, provided it can be shown, and the proofs are ample, that an insect is avoided owing to inedible qualities, what can be more natural than that resemblance to that insect should provide a measure of protection. If such a creature as a mantis can so far depart from its normal form as to resemble nothing so much as an animated vegetable, if an insect of one order can resemble another of a different order characterized by immense differences of structure, how much more easily may one butterfly come to resemble another, since half the difficulty is already surmounted by the similarity of form due to the possession of features which are common to the members of its own order. It should be recognized that mimicry between butterflies is not a thing apart, an exceptional phenomenon without parallel, but is merely another manifestation of a process of nature which is illustrated by many varying examples, all of which may be included under the general term mimicry, and all tending by various means to preserve the species involved.

In these pages I have endeavoured to give a concise account of butterfly mimicry and the considerations which have arisen therefrom. I should be the last to assert that any finality has been reached in the study of this fascinating subject. Indeed it is only now beginning to be understood, and whilst I have supported the theories which in the present state of our knowledge seem best adapted to the facts, I realize that there are still many difficulties, for the elucidation of which further study and experiment is required. It is my cherished hope that, with the present work as a guide, collectors and naturalists, especially those abroad, will find an additional interest in the study of the bionomics of butterflies. There remains

yet an unlimited field for actual experiments, especially those relating to the phenomenon of polymorphism, and to the question of comparative distastefulness. Careful observation on the habits of birds and other insectivorous creatures will yield information of the greatest value. Breeding experiments on a large scale are in the highest degree desirable. We are unacquainted with the larval stages of many of even the commonest butterflies, and the systematic determination of species would be greatly facilitated by notes on these subjects. The case of *Papilio dardanus* serves to show the surprises which are doubtless in store for those who have the opportunity of working out bionomic questions in the field. If, guided by the information here assembled, naturalists both at home and abroad will endeavour to collect not only butterflies but also the knowledge which a study of their relations in nature may reveal, then my work, in spite of its many imperfections, will not be entirely without an excuse for its existence.

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INDEX

Abantis tettensis, 103.
 Abdomen, 8.
abraxas, *P.*, 89.
acara, *A.*, *zetes* var., 66.
 larva and pupa of, 67.
acraea, *T.*, 42.
Acraea alciope, 44, 78, 79.
 alicia, 45.
 althoffi, 81.
 anemosa, 103.
 egina, 66.
 encedon, 35.
 esebria, 36, 41.
 jodutta, 36, 80.
 johnstoni, 47, 79.
 lycoa, 47.
 mima, 39.
 oberthüri, 82.
 orina, 69.
 perenna, 66.
 petraea, 41.
 praeponina, 88.
 proteina, 47.
 rogersi, 69.
 sotikensis, 46, 47.
 thalia, 20.
 viviana, 47.
 wigginsii, 40.
 zetes, 66.
 zetes var. *acara*, 66.
 zetes var. *jalema*, 66.
 zetes var. *pseudolydia*, 66.
Acraeas, offensive odour of, 35.
Acraeinae, 12.
acraeoides, *C.*, 69, note.
Acridiidae, both cryptic and warn-
 ing colours shown by, 88.
adamastor, *P.*, 53, 58.
aegyptius (*P.*), 24.
aequalis, *A. lycoa* f., 47.
aganice, *Pl.*, 73.
 larva and pupa of, 74.
agaristoides, *Ph.*, 44.
agatha, *N.*, 102.
agathina, *M.*, 83.
 larva and pupa of, 83.
 Aggressive mimicry, 15, 16.
 resemblance, 15, 16.

agrippina, *Ps.*, 43.
Alaena amazoula, 89.
albimaculata, *A.*, 56.
albinus, *D. chrysippus* var., 24.
Alcidis aurora mimicked by *P.*
 laglazei, 41, 124.
alciope, *A.*, 44, 78, 79.
 larva and pupa of, 46.
alcippina, *A. encendon* var., 35, 36.
alcippoides, *D. chrysippus* var., 24.
 H. misippus var., 30.
alcippus, *D. chrysippus* var., 24.
 Marshall on *D. chrysippus* var.,
 28.
Aletis helcita, 41.
 Alexander, Blakiston and, on the
 mathematical statement of
 Müller's hypothesis, 19, note.
alicia, *A.*, 45.
 Pl., 44, 45.
alcinoe, *Pl.*, 50, 77.
 Alluring coloration, 15, 16.
althoffi, *A.*, 81.
Amauris, neuration in, 8.
 albimaculata, 56.
 dannfelti, 55.
 echeria, 21, 56.
 echeria steckeri, 49, 57.
 egialea, 64.
 hecate, 55.
 hyalites, 54, 55.
 lobengula, 95.
 niavius, 54.
 ochlea, 54.
 psyttalea, 55.
 tartarea, 61, 63.
amazoula, *A.*, 89.
amenaida, *P.*, 88.
anacardii, *S.*, 63.
 Anatomy of butterflies, 8.
anemosa, *A.*, 103.
angustolimbata, *H.*, 61.
 Animal coloration, 15.
anneckeii (*T.*), 42.
 Antennae, structure of, 7.
 function of, 7, 8.
 of the *Bombycidae*, 8.
 value of, in classification, 7.

anthedon, *H.*, *dubius* var., 61.
antheus, *P.*, 53.
 Anticryptic colours, 16.
antimachus, *P.*, 68, note.
antinorii, *P. dardanus*, 91.
 Apatetic colours, 16.
apicalis, *M. darwinia* var., 80.
 Aposematic colours, 16.
argia, *E.*, 85.
Argynnis hyperbius, 38.
 inconstans, 38.
argyrius, *A.*, 38.
Aroa punctifera, 103.
Arrugia, 12, note.
Asilidae, 18.
asphodelus, *M.*, 86.
aspidos, *L.*, 90.
Atella phalantha, 76.
Aterica galene, 64.
aurivillii, *A. alciope* f., 44, 78.
 Aurivillius, Professor Chr., 11.
 on forms of *P. dardanus*, 102,
 note.
aurora, *Al.*, 41, 124.
 Baboons, Marshall's experiments
 with, 117.
bammakoo, *E.*, 50.
Baoris netopha, 103.
bartteloti, *H. dinarcha* var., 64.
 Bates, H. W., observations on
 resemblances of moths to in-
 sects of other orders, 14.
 observations on South American
 Lepidoptera, 14, 17.
 on structure of butterflies' legs,
 10, 11.
 on the value of the study of
 butterflies, 17.
 Batesian mimicry, 17.
Belenois thysa, 84.
bernice, *M.*, 90.
 Berries, poisonous, 22.
bertha, *Pl.*, 73.
 Betham, J., on *A. hyperbius*, 39.
bewsheri, *H. dubius* ab., 61.
 Bibliography, 127.

- biblis*, C., 39.
bicolor, *Ps. eurytus* ab., 71, 72.
bidentata, O., edibility of larva varying with food plant, 113.
bimacula, T., 43.
 Birds attacking butterflies, alleged paucity of recorded instances of, 106.
 eating butterflies, 120-3.
 eating butterflies, indirect evidence of, 122.
 lack of instinctive likes and dislikes in, 123.
 Marshall's experiments with, 116.
 Blakiston and Alexander on the mathematical statement of Müller's hypothesis, 19, note.
boisduwali, H., 91.
Ps., 67.
boisdvallianus, P., 72.
bolina, H., 30, 31.
Bombycidae, antennae of, 8.
bonasia, A., 82.
brasidas, P. *leonidas* var., 52.
Brassolinae, 12.
braunei, A. *encedon* var., 35.
brenda, L., 90.
 Brimstone butterfly, 13.
brutus, P., 92, 99.
 Bugs, eaten by baboons, 117.
 Butler, A. G., experiments in distastefulness by, 110.
 Butterflies a guide to the study of evolution, 16.
 African, eaten by birds, 121.
 eaten by birds, 120-3.
 eaten by birds, indirect evidence of, 122.
 eaten by kestrel, 121.
 evidence of the unpalatability of certain, 109-19.
 Indo-Malayan, eaten by birds, 122.
 Nearctic, eaten by birds, 122.
 Neotropical, eaten by birds, 122.
 Palearctic, eaten by birds, 121.
 tenacity of life in distasteful, 109.
 Byatt, H. A., on proportions of *Ps. poggei* to *D. chrysippus*, 34.

cacica, *Morpho*, 13.
caecilia, A. *encedon* var., 35.
caffra, A., 66.
Caligo, 14.
camerunica, Pl., 77.
cardui, *Pyrameis*, 24.

carmentis, A., 81.
cassiopea (E.), 85.
Castnia, 18.
 Poulton's observations on, 124.
Catochrysops mashuna, 103.
 Cells, Schaeffer on hypodermal, 10.
cenea, P., 92, 100.
cerberus, H. *dubius* var., 61.
Cethosia penthesilea, 39.
biblis, 39.
chanleri, Pl., 73.
Charaxes, 103.
acraeoides, 69, note.
charmian, M., 88.
chlorana, A., 76.
chriemhilda, E., 41.
chrysippus, *Danaida*, 24.
 chasing female *H. misippus*, 31.
 flirting with *Ps. poggei*, 35.
 in company with female *H. misippus*, 32.
 larva of, 25.
 Poulton on the origin of the forms of, 27, 28.
 pupa of, 25.
 pursued by male *H. misippus*, 32.
 scent of, 30.
 unpalatability of larva of, 30.
 Wood-Mason on pupa of, 25.
Citrinophila erastus, 90.
similis, 89.
clarki, *Ps.*, 69.
 Classification, 7, 10.
 Antennae, value of, in, 7.
 importance of legs in, 8.
 table of, 11.
cleodora, E., cryptic appearance of, 85.
 Coloration, alluring, 15, 16.
 sexual, 15.
 synaposematic, 16.
 Colour fading in *Acraeas* and their mimics, 66.
 fading in *P. ridleyanus*, 69.
 interchangeability of, 29.
 Colours of animals, Poulton on, 15.
 anticryptic, 16.
 apatetic, 16.
 aposematic, 16.
 combination of cryptic and warning colours in *Eronia* and other insects, 88.
 cryptic, 16.
 epigamic, 16.
 episematic, 16.
 of animals, table of the, 16.

 Colours of animals (*continued*).
 not the result of chance development, 23.
 procryptic, 16.
 pseudaposematic, 16.
 pseudepisematic, 16.
 pseudosematic, 16.
 sematic, 16.
 signalling, 15.
 true warning, 16.
 warning, 15.
columbina (A.), 76.
colvillei, A. *boisduwali* var., 67.
 Conclusions, General, 124.
concordia, C., 70.
confusa, A. *johnstoni* f., 47.
conradi, *Ps.*, 74, note.
consanguinea, Pl., 66.
 Convergent mimicry, 21.
Cooksonia trimeni, 40.
corrineus, P., 53.
cratippus, *Danaida*, 24, 39.
crawshayi, C., 70.
 E., 44.
Crenidomimas concordia, 70.
Crenis pecheuli, 70.
rosa, 70.
 Crimson underwing, 13.
crowleyi, E., 43.
 Cryptic colours, 16.
cupavia, A., 64.
 Curtis, P., observations on kestrel, 121.
cydonia, A., 44.
Cymothoe, 43.
cynorta, P., 50, 59.
 gynandromorphous form of, 72.
cynthius, A., 82 and note.
cypris, *Morpho*, 13.

daira, A. *encedon* var., 35, 36.
damocles, A. *psytalea* f., 55.
damoclina, H., 61.
Danaida, 8.
chrysippus, distribution of the forms of, 26.
chrysippus, 24.
cratippus, 24, 39.
genulia, 39.
petilia, 39.
Danainae, 11.
dannjelli, A., 55.
dardanus, P., 22, 59, 92, 99.
 Mrs. Barber on cryptic habits of male of, 98.

- dardanus*, *P.* (continued).
 captured by bird, 98.
 cryptic appearance of larva of, 97.
 G. F. Leigh on difficulty of finding larvae of, 98.
 M. Weale on flight of, 98.
 process of change from larva to pupa of, 97.
 resemblance of pupa of, to a leaf, 98.
 Surg.-Capt. W. G. Clements on cryptic habits of male of, 98.
- Darwin, 15.
- darwinia*, *M.*, 37, 80.
- Dead leaf butterflies, 13.
- deceptor*, *H.*, 57.
- deficiens*, *Ps. boisduvali* ab., 67.
- Deloneura immaculata*, 103.
- millari*, 103.
- deludens*, *H.*, 57.
- demodocus*, *P.*, 53.
- Diaposematism, 21, note.
- dichroaria*, *P.*, 89.
- Diestogyna*, 40.
- karschi*, 41.
- tadema*, 41.
- veronica*, 41.
- difficilis*, *A.*, 55.
- dinarcha*, *H.*, 60, 63.
- var. *bartteloti*, 64.
- diocippus*, *H.*, 30.
- dionysos*, *P. dardanus* f., 92, 99.
- Dioptis*, 18.
- Distastefulness in butterflies, 109-19.
- experiments in, by A. G. Butler, 110.
- by H. Eltringham, 113.
- by F. Finn, 113.
- by G. A. K. Marshall, 114-19.
- by M. de Nicéville, 113.
- by Professor F. Plateau, 118.
- by Professor Poulton, 111.
- by J. Weir, 110.
- by Professor Weismann, 110.
- by Professor W. M. Wheeler, 118.
- origin of, in the larval stage, 112.
- Distastefulness not absolute, 23.
- Distastefulness of insects to human beings, 118.
- Dixey, Dr. F. A., groups of mimetic *Pierinae* exhibited by, 87.
- on mimetic attraction, 20, 31.
- on scent of *D. chrysippus*, 30.
- Doflein, Dr. F., on birds eating butterflies, 121.
- dohertyi*, *M. marshalli* f., 37, 38.
- dominicanus*, *A. niavius* f., 54.
- dorippoides*, *H. misippus* var., 30.
- P. cenea* var., 92, 101.
- dorippus*, *D. chrysippus* var., 24.
- confusion of *klugii* with, 25.
- drucei*, *H. dubius* var., 61.
- dubius*, *H.*, 61.
- larva and pupa of, 63.
- duodecimpunctata* (*Ps.*), 76.
- echeria*, *Amauris*, 21, 56.
- influence of *A. psyttalea* on, 57.
- larva and pupa of, 56.
- steckeri*, *A.*, 49, 57.
- echerioides*, *P.*, 59.
- egialea*, *A.*, 55, 64.
- egina*, *A.*, 66.
- eleus*, *E.*, 42.
- Ellis, Captain, on *H. misippus* at sea, 32.
- elongata*, *Pl.*, 75.
- Elsa morgeni*, 65.
- Elymnias bammakoo*, 50.
- phegea*, 50, 79.
- encedon*, *Acraea*, 35, 81.
- geographical distribution of, 36.
- larva and pupa of, 37.
- mistaken for *D. chrysippus*, 37.
- scent of, 36.
- encedonia* (*A.*), 35.
- Environment as a cause of resemblance, 107.
- epaea*, *Pl.*, 50, 71.
- Epigamic colours, 16.
- epigea*, *Ps.*, 71, 72.
- Episematic colours, 16.
- epitellus*, *Pl.*, 80.
- Epitola honorius*, 91.
- erasmus*, *C.*, 90.
- erastus*, *C.*, 90.
- Eronia argia*, 85.
- cleodora*, cryptic appearance of, 85.
- combination of cryptic and aposematic colours in, 88.
- mimicry of Danaine butterflies by Oriental species of, 88.
- thalassina*, 86.
- Erycinidae*, 11, 12.
- Erycininae*, 12.
- esebria*, *A.*, 36, 41.
- similarity of varieties of *A. jodutta* and, 81.
- eudoxia* (*M.*), 85.
- Eueides pavana*, 20.
- Euphaedra*, 103.
- crawshayi*, 44.
- eleus*, 42.
- eusemoides*, 44.
- ruspina*, 42.
- zaddachi*, 44.
- zampa*, 42.
- Euploea*, 50.
- Euptera crowleyi*, 43.
- Euralia*, 62 and note.
- (*Hypolimnas*) *mima*, 21.
- mima* and *A. echeria*, Marshall on, 21.
- eurita*, *A.*, 75.
- Euryphene*, 103.
- chriemhilda*, 41.
- senegalensis*, 41.
- euryta*, *Pl.*, 70.
- Ps.*, 71.
- eurytus*, *Ps.*, 71.
- D.*, 71, 75.
- Eusemia falkensteinii*, 41.
- eusemoides*, *E.*, 44.
- Euterpe*, 18.
- Euxanthe tiberius*, 102.
- wakefieldi*, 52, 102.
- Evolution, butterflies as a guide to, 16.
- excisa*, *Pl.*, 44, 78.
- expansa*, *Ps. lucretia* var., 58.
- Eyes of butterflies, structure of, 7.
- falkensteinii*, *Eu.*, 41.
- fallax*, *A. lycoa* f., 47.
- Female mimicry, Poulton on, 22.
- Wallace's explanation of, 22.
- Femur, 8.
- Finn, F., experiments in distastefulness by, 113.
- flava*, *A.*, 80.
- flaveola*, *C.*, 90.
- flavescens*, *A. proteina* f., 47.
- Fletcher, T. B., on *A. hyperbius*, 39.
- floricola*, *T.*, 89, note.
- formosa*, *M.*, 51.
- Pl.*, 65.
- fulva* (*A.*), 35.
- fulvaria*, *M.*, 44, 46.
- Ps.*, 65.
- fulvescens*, *A. proteina* f., 47.
- galene*, *A.*, 64.
- gallienus*, *P.*, 72.
- gazengeli*, *Ps.*, 76.

- gea*, Pl., 71.
Ps., 71.
genutia, D., 39.
Geodena, 103.
godmani, Pl., 77.
gottbergi, *Ps.*, 76, 78, note.
 Great Pyramid, *Pyrameis cardui* on, 24.
Grypocera, 11.

hanningtoni, *A. albimaculata* f., 56.
Haustellum, 8.
hecate, A., 55.
hegemone, *Ps.*, 76.
helcita, A., 41.
helcitolides, P., 41.
Heliconidae, Bates on, 109.
Heliconinae, 12, 20.
heliogenes, *Ps. lucretia* var., 58.
 Heron, F. A., views of, on size in relation to mimicry, 69, note.
Hesperidae, 7, 11, 13.
 Hewitson, W. C., and *Pseudacraea eurytus*, 71.
C. erastus described as a *Pieris* by, 90.
 his disbelief of Trimen's views on *P. dardanus* (*merope*), 93.
 on colour selection in butterflies, 105.
Hewitsonia boisduvali, 91.
Hibrildes neavei, 103.
hippocoon, P., 92, 99.
hippocoonides, *P. cenea* var., 92, 100.
hirce, *Ps.*, 71.
hobleyi, *Ps.*, 77.
homeyeri, P., 59, 60.
L., 90.
 Homoeochromatism, Blandford on, 105.
 Hopkins, Professor F. G., on interchangeability of colour in *Pieridae*, 29
 on pigments in *Pieridae*, 10.
horta, A., quarrelsomeness of, 35.
humbloti, *P. dardanus*, 91, 99.
hyalites, A., 54, 55.
Hyelosia, 18.
hyperbius, A., 38.
 Betham on, 39.
 de Nicéville on, 39.
 Walker on, 39.
 Hypertely, 105.
Hypolimnas anthedon, 61.
bewsheri, 61.

Hypolimnas (continued).
bolina f. *nerina*, 31.
deceptor, 57.
deludens, 57.
dinarcha, 59, 63.
dubius, 61.
drucei, 61.
imperialis, 64.
kirbyi, 57.
mima, 61.
misippus, 30.
 neuration in genus, 8, 10.
usambara, 63, 64.
wahlbergi, 61.

idotea (E.), 85.
ilione, *Ituna*, 18.
imitator, *Ps.*, 74.
 appearance of, in life, observed by Colonel Bowker, 74.
immaculata, D., 103.
 Immunity, regrettable use of the term, 107.
imperialis, H., 64.
inaria, *H. misippus* var., 30.
inconstans, A., 38.
 Independent creation, the doctrine of, 15.
infusata, 35, 36.
intermedia, E. *phegea* var., 50.
interniplaga, *P. leonidas* ab., 52.
iris, D., 40.
Isoglossa woodii, 85.
isokani, Ph., 84.
Ithomeis, 18.
Ithomiæ, 18.
Ituna ilione, 18.

jacksoni, *A. echeria* f., 56, 57.
P., 59.
jalema, *A. zetes* var., 66.
jaopura (M.), 85.
jodutta, A., 36, 80.
 similarity of varieties of *A. esebria* and, 81.
johnstoni, A., 47.

Kallima paralekta, Wallace on habits of, 13.
karschi, *A. viviana* var., 47.
karschi, D., 41.
Kedestes macomo, 103.
 Kennel Professor, observations on garden warbler, 121.

khara, A., 66.
kilimandjara, *A. lycoa* f., 47.
kirbyi, H., 57.
P., 103.
klugii, confusion of *dorippus* with, 25.
krausi, M., 88.
künowi, *Ps.*, 77, 78.

 Labium, 8.
 Labrum, 8.
laglazei, P., 41, 124.
larima, B., 84.
Larinopoda aspidos, 90.
brenda, 90.
lircea, 90.
tera, 90.
latifasciata, Pl., 49.
laudonius (A.), 76.
 Legs, 8.
 importance of, in classification, 8.
 Leigh, G. F., his breeding experiments with *P. dardanus*, 94.
H. misippus bred by, 31.
 on unpalatability of larvae of *D. chrysippus*, 30.
Leptalis, 18.
leonidas, P., 52.
leonora (T.), 52.
lermanni, N., 103.
Libytheinae, 12.
 Light, actinic effect of, 29.
limniæ (T.), 52.
lircea, L., 90.
Limenitis, mimicry in American species of, 107.
Liptena homeyeri, 90.
 Lizards, experiments with, 110, 111, 112, 113, 114.
 and Frogs, Marshall's experiments with, 116.
 Poulton's experiments with, 111.
lobengula, A., 95.
 Lock, R. H., on mimicry, 104.
 Longstaff, on *P. leonidas*, 53.
 on scent of *D. chrysippus*, 30.
lucretia, *Ps.*, 53, 58.
Lycaenidae, 11, 12, 37.
 further instances of mimicry in, 88.
 neuration in, 10.
lycia, *A. encedon* f., 35, 36.
 Marshall on, 36.
lycoa, A., 47.
 larva and pupa of, 48.

- macaria*, Pl., 46.
macarina, A., 44.
macarista P., 77.
macomo, K., 103.
madagascariensis, H., 61.
Mandibles, 8.
Mania typica, distastefulness of larva of, &c., 111.
Mantidae, Marshall's experiments with, 114.
marginalis, C., 89.
H., 61.
Marshall, G. A. K., on *D. chrysippus* var. *alcippus*, 28.
experiments in distastefulness, 114-18.
experiments with forms of *Precis*, 79.
on *E. mima* and *A. echeria*, 21.
on habits of *Ps. boisduvali trimeni*, 68.
on *H. mima* and *H. wahlbergi*, 61.
on juice exuded by *Pl. aganice*, 74.
on *P. leonidas*, 53.
marshalli, M., 35, 37.
Marshall's discovery of, 37.
photographed by Neave, 38.
mashuna, C., 103.
Maxillae, 8.
megisto, *Thyridia*, 18, 19.
Meldola, Professor R., on Müllerian mimicry, 22.
Packard's error pointed out by, 106.
translation of Müller's paper by, 19.
meldolae, 84.
Melinda formosa, 51.
mercedonia, 51.
morgeni, 65.
Mendelism, 62, note.
menippe, A., 66.
menthastri, S., 110.
mercedonia, M., 51.
meriones, P., 91, 99.
merope, P., 92, 99.
metaplanema, Ps., 75.
Millar, A. D., his breeding experiments with *H. deceptor*, 58.
on breeding *H. mima* and *H. wahlbergi*, 62.
millari, D., 103.
milonia, Pr., 79.
mima, A., 39.
Euralia (Hypolimnas), 21, 61.
Mimacraea charmian, 88.
darwinia, 37, 80.
fulvaria, 44, 46.
krausi, 88.
marshalli, 35, 37.
neavei, 82.
neokoton, 88.
neurata, 88.
poultoni, 46, 47.
skoptoles, 38.
Mimetic attraction, 31.
Dixey on, 20.
resemblance still in process of development, 107.
mimeticus, P., 51.
Mimicry, aggressive, 15, 16.
Batesian, 17.
convergent, 21.
discussed at the Entomological Society, 105.
further instances of, in *Lycaenidae*, 88.
further instances of, not illustrated on the plates, 102.
F. A. Heron on size in relation to, 69, note.
in American species of *Limenitis*, 107.
in relation to sex, 22.
in the *Pierinae*, 83.
R. H. Lock on, 104.
Lycaenid, prevalence of, in Africa, 42.
more perfect in male than female, Instance of, 67.
Müllerian, 19.
not produced by environment, 124-5.
produced by Natural Selection, 124-5.
protective, 15.
misippe, H., 39.
misippus, H., 30.
bred by Leigh, 31.
female chased by *D. chrysippus*, 31.
female in company with *D. chrysippus*, 32.
geographical distribution of forms of, 33, 34.
geographical range of, 31.
larva of, 32.
male pursuing *D. chrysippus*, 32.
pupa of, 32.
regarded as a Müllerian mimic, 33.
taken at sea, 32.
mixta (E.), 85.
montana, Pl. *aganice* f., 73.
Morgan, Professor L., on instincts of young birds, 123.
morgeni, E., 65.
M., 65.
Morphinae, 12.
neururation in, 9.
structure of scales in, 10.
Morpho cacaica, 13.
cypris, 13.
Mouth parts of butterflies, 8.
Muir, F., observations on butterfly-eating mantis, 114.
Müller, Dr. F., on the resemblance between butterflies of protected genera, 19.
Müller's hypothesis, Meldola's translation of, 19.
Müllerian mimicry, 19.
mycenaea, A., 66.
Mylothris agathina, 83.
asphodelus, 86.
bernice, 90.
distastefulness of, 87.
spica, 85.
trimenia, 87.
natalensis, Pr., 79.
Neave, S. A., on the appearance of *Ps. hegemon*, 76.
on appearance of *L. homeyeri*, 90.
on *Crenidomimas concordia*, 70.
on *Diestogyna iris*, 40.
on habits of *Crenis pechueli*, 70.
on mimetic species of *Euphaedra*, 44.
on model of *P. leonidas*, 54, note.
on *P. rex* and *P. mimeticus*, 51.
neavei, H., 103.
M., 82.
necoda, A. *encedon* var., 35, 36.
nelsoni, Pl., 77.
neokoton, M., 88.
neptidina, Ps., 102.
Neptidopsis ophione, 102.
Neptis agatha, 102.
lermanni, 103.
woodwardi, 103.
nerina, H. *bolina* var., 31.
netopha, B., 103.
neumanni, P., 60.
neurata, M., 88.

- Neuration. English and German methods compared, 10.
 in genus *Amauris*, 8.
 in genus *Hypolimnas*, 9, 10.
 in *Lycaenidae*, 10.
 in *Morphinae*, 9.
 in *Papilionidae*, 9, 10.
 in *Pieridae*, 10.
 nomenclature of, 8.
 System of, by numbers, 10.
- Neuroxena*, 103.
- niavices*, A., 54.
- niavioides*, *P. antinorii* var., 91, 99.
- niavius*, A., 54.
- P.*, 92.
- Nicéville, M. de, experiments in distastefulness, 113, on *A. hyperbius*, 39.
- nigra*, Ps., 43.
- nigroapicalis*, A. *orina* ab., 69.
- niobe*, *P. dardanus* var., 92.
- nioboides*, *P. dardanus* var., 92.
- niphe*, A., 38.
- nyanza*, T., 43.
- Nyctemera*, 102.
- Nymphalidae*, 11.
- Nymphalinae*, 12.
- oberthürri*, A., 82.
- Objections to mimetic theories, 104.
- ochlea*, A., 54.
- Odontopera bidentata*, edibility of larvae varying with food-plant, 113.
- ophione*, N., 102.
- oreta*, A., 69.
- orina*, A., 69.
- orinata*, A. *orina* ab., 69.
- Ornithoptera*, 13.
- Packard, Professor A. S., criticism of the Bates-Müller theories by, 106.
- Palpi, 8.
- Papilio*, 9, 17.
- adamastor*, 53, 58.
- antheus*, 53.
- antimachus*, 68, note.
- antinorii*, 91, 99.
- cenea*, 92, 100.
- corinneus*, 53.
- cynorta*, 50, 59, 72.
- dardanus*, 22, 59, 92, 99.
- dardanus antinorii*, 99.
- dardanus cenea*, 100.
- Papilio* (continued).
- dardanus dardanus*, 99.
- dardanus humbloti*, 99.
- dardanus polytrophus*, 92, 101.
- dardanus tibullus*, 92, 100.
- demodocus*, 53.
- echerioides*, 59.
- gallienus*, 73.
- homeyeri*, 59, 60.
- humbloti*, 91, 99.
- jacksoni*, 59.
- laglazei* mimicking a moth, 41, 124.
- leonidas*, 52.
- meriones*, 91, 99.
- mimeticus*, 51.
- policenes*, 53.
- preussius*, 60.
- rex*, 51.
- ridleyanus*, 66, 69.
- similis*, 52.
- zoroastres*, 60.
- Papilionidae*, 10, 11, 13.
- neuration in, 9, 10.
- paragea*, P., 73.
- Parallel variation, 105.
- Pardopsis punctatissima*, 89.
- pavana*, *Eueides*, 20.
- pechueli*, C., 70.
- peculiaris*, *P. cynorta* f., 72.
- pelopidas*, *P. leonidas* ab., 52.
- penthesilea*, C., 39.
- Pentila abraxas*, 89.
- amenaida*, 88.
- kirbyi*, 103.
- tropicalis*, 89.
- perenna*, A., 66.
- Pericopinae*, 41.
- Pericopsis*, 18.
- perlucens*, Ph., 87.
- persephone*, A., 66.
- petilia*, D., 39.
- petiverana*, T., 51, 52.
- Petovia dichroaria*, 89.
- petraea*, A., 41.
- Phaegorista similis*, 41, 103.
- agaristoides*, 44.
- Phalaenae*, 7.
- phalantha*, A., 76.
- phalanthus* (A.), 76.
- phegea*, E., 50, 79.
- phileris*, M., 86.
- phoebe*, Ph., 84.
- Phrissura lasti*, 87.
- perlucens*, 87.
- phoebe*, 84.
- sylvia*, 86.
- Pieridae*, 11, 12, 20.
- mimicry in, 83.
- neuration in, 10.
- Professor Hopkins on pigments of, 10.
- Pieris*, 18.
- Pinacopteryx rubrobasalis*, 84.
- plagioscia*, P.
- Planema aganice*, 73.
- f. montana*, 73.
- alicia*, 44, 45.
- alcinoe*, 50, 77.
- camerunica*, 77.
- consanguinea*, 66.
- elongata*, 75.
- epaea*, 50, 71.
- excisa*, 44, 78.
- formosa*, 65.
- gea*, 71.
- godmani*, 77.
- latifasciata*, 49.
- macaria*, 46.
- macarista*, 77, 78.
- paragea*, 73.
- plagioscia*, 77.
- poggei*, 45, 50, 77, 78.
- telekiana*, 47.
- tellus*, 36, 50, 80.
- salvini*, 44, 45, 77.
- vestalis*, 70.
- planemoides*, *P. dardanus* var., 92, 79, 100.
- gynandromorphous form of, 96.
- Plateau, Professor F., experiments in distastefulness, 118.
- poggei*, Pl., 45, 50, 77.
- geographical coincidence of mimics of, 79.
- Pseudacraea*, 34, 38.
- Ps., flirting with *D. chrysippus*, 35.
- Pseudacraea*, proportion of, to model, 34.
- X., 41.
- Poisonous berries, 22.
- policenes*, P., 53.
- polytrophus*, *P. dardanus*, 92.
- Poulton, Professor E. B., on colours of animals, 15.
- experiments in distastefulness by, 111.
- on female mimicry, 22.
- on forms of *P. dardanus* and *A. johnstoni*, 48.
- on habits of larva of *M. typica*, 111.

- Poulton, Professor E. B. (*contd.*)
on mimicry in American species of *Limenitis*, 107.
on *Neptis woodwardi*, 103.
on prevalence of Lycaenid mimicry in Africa, 42.
on species of *Castnia*, 124.
on the forms of *P. dardanus*, 94.
on the origin of forms of *D. chrysippus*, 27, 28.

poultoni, M., 46, 47.
poppea, M., 86.
(E.), 85.
praeponina, A., 88.
Precis, 32.
milonia, 79.
natalensis, 79.
rauana, 79.
simia, 79.
sesamus, 79.
praeussius, P., 60.
Procryptic colours, 16.
pronuba, T., eggs of, eaten by earwig, 111.
Protective mimicry, 15.
resemblance, 15, 16.
proteina, A., 47.
Protogonius, 18.
protracta, Ps. *lucretia* var., 58.
Pseudacraea boisduvali, 67.
clarki, 69.
conradti, 74, note.
eurytus, 71.
fulvaria, 65.
gottbergi, 76, 78, note.
hobleyi, 77, 78.
imitator, 74.
künowi, 78.
lucretia, 53, 58.
mimetic tendencies of, 34.
poggei, 34, 38.
rogersi, 74.
ruhama, 75.
simulator, 78.
striata, 71.
terra, 80.
Pseudaletis agrippina, 43.
nigra, 43.
Pseudoposematic colours, 16.
Pseudargynnis hegemon, 76.
Pseudathyma neptidina, 102.
Pseudepisematic colours, 16.
pseudolycia, A. *zetes* var., 66.
Pseudosematic colours, 16.
psytalea, A., 55.
influence of, on *A. echeria*, 57.
punctatissima, P., 89.
punctifera, A., 103.
Pyrameis cardui, 24.
rauana, Pr., 79.
rechila, P., 92.
Recognition marks, 16.
Red Admiral butterfly, 13.
Resemblance, accidental, 106.
aggressive, 15, 16.
between butterflies of protected genera, 19.
of butterflies to leaves, 13.
of *Caligo* to an owl, 14.
of a moth to a snake, 14.
protective, 15, 16.
rex, P., 51.
rhodope (Ph.), 86.
ridleyanus, P., 66, 69.
described as a female *Acraea*, 69, note.
Rogers, K. St. A., on *A. ochlea*, 54.
on appearance of female Ps. *rogersi*, 75.
on habits of Ps. *boisduvali trimeni*, 68.
on *H. usambara*, 64.
on the habits of *Pentila amenaïda*, 89.
rogersi, A., 69.
Ps., 74.
Romalaeosoma, 42.
rosa, C., 70.
Rosenberg, W. F. H., on habits of *Caligo*, 14, note.
rubrobasalis, Pin., 84.
rubrofasciata, A., 81.
rudolphina, A., 66.
ruhama, Ps., 75.
ruspina, E., 42.
ruspinae, P. *antinorii* var., 91, 99.
sabrata (B.), 84.
Salamis anacardii, 63.
salvini, Pl., 44, 45, 78.
sanguinea, T., 42.
Satyrinae, 11.
Scales, structure of, 10.
Scapulae, 8.
Schaeffer on hypodermal cells, 10.
schecana, A. *alciope*, 44, 45.
Selection, sexual, F. Müller on, 105.
Sematic colours, 16.
semialbescens, A. *proteina* f., 47.
semiflava (E.), 85.
semifulvescens, A. *proteina* f., 47, 79.
senegalensis, E., 41.
T., 89.
sesamus, Pr., 79.
Sex, mimicry prevalent in the female, 22.
Sexual coloration, 15.
sganzini, A. *encedon* var., 35, 36.
Sharp, Dr., 11.
views on mimicry of, 107.
his views not specially applicable to mimetic theories, 108.
Signalling colours, 15.
simia, Pr., 79.
similis, C., 89.
P., 52.
Ph., 41, 103.
simulator, Ps., 78.
Size in relation to mimicry, F. A.
Heron on, 69, note.
skoptoles, M., 38.
Smell, the sense of, in human beings, 119.
Sir Michael Foster on the sense of, 119.
sotikensis, A., 46, 47.
soyauxii, L., 90.
spica, M., 85.
pupa of, 85.
Spiders, Marshall's experiments with, 115.
Spilosoma menthastri, 110.
Spiracles, 8.
steckeri, A. *echeria*, 49, 56, 57.
striata, Ps., 71.
sulfurea P., 92, 99.
sulphurea (E.), 85.
sulpitia (Ps.), 58.
sylvia, Ph., 86.
Synaposematic coloration, 16.
tadema, D., 41.
tanganikae, P., 60.
tarquinia, Ps. *lucretia* var., 58.
tartarea, A., 61, 63.
Telipna acraea, 42.
nyanza, 43.
sanguinea, 42.
telekiana Pl., 47.
tellus, Pl., 36, 50, 80.
tephnia, A., 38.
tera, L., 90.
Tereas senegalensis, 89.
Teriomima xantha, 89.

- terra*, Ps., 80.
tettensis, A., 103.
thalassina, E., 86.
thalia, *Acraea*, 20.
 Thayer, A. H., his views on animal coloration, 106.
 Theban fresco, butterflies depicted on, 24.
theophane, A. *galene* var., 64.
 Thorax, 8.
Thyridia megisto, 18, 19.
thysa, B., 84.
tiberius, E., 102.
tibullus, P. *dardanus*, 92.
tirikensis, Ps., 78.
Tirumala petiverana, 51, 52.
 Tortoiseshell butterfly, 13.
toruna, A. *johnstoni* f., 47.
 Tracheae, 8.
tricolor Ps., 43.
 Trimen, R., on the appearance of *M. trimenia*, 87.
 his discovery of the forms of *P. dardanus* (*merope*), 93.
 on habits of *M. agathina*, 84.
 on habits of *Saturniidae*, 88, note.
 on mimicry in the Ethiopian region, 22.
 on *P. leonidas* f. *brasidas*, 53.
 on pupa of *P. leonidas*, 53.
 on tenacity of life in butterflies, 109.
 on the distastefulness of African butterflies, 109.
 views on *Planema montana*, 73, note.
trimeni, A. *boisduvali* var., 67.
 C., 40.
 P. dardanus cenea var., 92, 100.
 P. dardanus polytrophus var., 92, 101.
trimenia, M., 87.
trophonius, P. *dardanus cenea* var., 92, 100.
trophonius, P. *dardanus* var., pupa of, 98.
tropicalis, P., 89.
 True warning colours, 16.
Tryphaena pronuba, eggs of, eaten by earwig, 111.
typica, M., distastefulness of larva of, &c., 111.
usagarae (A.), 35.
usambara, H., 63, 64.
vaillantina, A., 56.
varia, E. *argia* var., 85.
veronica, D., 41.
verulanus, E., 86.
vestalis Pl., 70.
viviana, A., 47.
wakefieldi, E., 52, 102.
wahlbergi, H., 61.
 Walker, Com. J. J., *A. hyperbius*, 39.
 Wallace, A. R., 15.
 explanation of female mimicry, 22.
 on distastefulness in butterflies, 110.
 on habits of *Kallima paralekta*, 13.
 on mimicry in the eastern tropics, 22.
 Warning colours, 15.
 false, 16.
 true, 16.
 Weale, M., his breeding experiments with *P. dardanus* (*merope*), 94.
 Weir J., experiments in distastefulness, by, 110.
 Weismann, Professor, experiments in distastefulness, by, 110.
 Wheeler, Professor W. M., experiments in distastefulness, by, 118.
wigginsii, A., 40.
 Wings, 8.
 causes of transparency in, 10.
 structure of, in butterflies, 10.
 Wood-Mason, views on forms of pupa of *D. chrysippus*, 25.
woodwardi, N., 103.
xantha, T., 89.
Xanthospiloptyx, 44.
Xanthospiloptyx poggei, 41.
 Yellow underwing, 13.
 Yerbury, Colonel, on the forms of *D. chrysippus*, 26, 27.
 observations on butterfly-eating mantis, 114.
 Young birds, inability to discriminate between suitable and unsuitable foods, 22.
zaddachi, E., 44.
zampa, E., 42.
zeryntius, P., 72.
zetes *Acraea*, 66.
 larva and pupa of, 67.
zethea, A., 66.
zethes, A., 66.
zidora, A., 66.
zoro astres, P., 60.

PLATES

EXCEPT WHERE OTHERWISE STATED THE FIGURES ARE DRAWN FROM EXAMPLES
IN THE AUTHOR'S COLLECTION.

PLATE I

FORE-TARSI OF REPRESENTATIVE FAMILIES OF BUTTERFLIES

FIG. 1. NYMPHALIDAE. *Hypolimnas misippus*, Linn. ♀. The joints though visible are greatly reduced, and there is an entire absence of claws. In many Nymphalid butterflies the last joint appears somewhat swollen and the spines are generally visible even to the naked eye.

FIG. 2. NYMPHALIDAE. *Hypolimnas misippus*, ♂. There is no trace of joints and the tarsus is clothed with fine hairs. These characteristics are very typical and the sex of most Nymphalid butterflies may be determined by an examination of these characters.

FIG. 3. ERYCINIDAE. *Abisara savitri*, Feld. ♀. The joints and claws are present, though small, and the claws are not always easy to observe.

FIG. 4. ERYCINIDAE. *Abisara savitri*, ♂. Joints and claws still absent. The ♂ Erycinid fore-foot is frequently distinguishable from that of the ♀ by the exceptional growth of hair, which gives it a thick brush-like appearance.

FIG. 5. LYCAENIDAE. *Lycaena icarus*, Scop. ♀. The joints and claws are well developed.

FIG. 6. LYCAENIDAE. *Cupido zoë*, Reak. ♂. The tarsus is still exarticulate and devoid of claws, though strongly spined on the underside. In some male *Lycaenidae* one claw is present. In the aberrant African genus *Arrugia*, Wall., the male fore-tarsi are jointed and armed with two claws.

FIG. 7. PIERIDAE. *Ganoris rapae*, Linn. ♂. The tarsi are complete and jointed in both sexes, and bear not only bifid claws but also the additional apparatus known as the pulvillus and paronychia.

FIG. 8. A more highly magnified view of the terminal joint of the above. There is no difference in the feet of the two sexes.

FIG. 9. PAPILIONIDAE. *Papilio echerioides*, Trim. ♀. The claws are simple and without appendages.

FIG. 10. PAPILIONIDAE. *Papilio dardanus cenea*, Stoll, ♂. The claws are simple, though the joints are somewhat longer than in *echerioides*.

FIG. 11. HESPERIDAE. *Tagiades fesus*, Fabr. ♂. The pulvillus is present and there is an appendage on the tibia, which is also found, however, in *Papilio*.

FIG. 12. HESPERIDAE. The same species. One of the hind-legs showing the second pair of spurs on the tibia.

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PLATE II

MODELS.

FIG. 1. *Danaida chrysippus*, Linn. ♂. Northern Rhodesia. The dark form typical of the African continent.

FIG. 2. *D. chrysippus*, ♀. Durban. An example of the golden-yellow ground-colour more usually found in Oriental examples.

FIG. 3. *D. chrysippus*, f. *alcippus*, Cr. ♂. A West African example, though the form also occurs in other localities.

FIG. 7. *D. chrysippus*, f. *dorippus*, ♂, Klug. Entebbe.

FIG. 9. *D. chrysippus*, f. *albinus*, Lanz. Dar-es-Salaam. It is interesting to note that the white sub-apical bar is still represented in this example by three pale spots in the ground-colour.

MIMICS.

FIG. 4. *Hypolimnas misippus*, Linn. ♀. Natal.

FIG. 8. *H. misippus*, ♀. Durban. The example shows the average ground-colour of the typical ♀.

(FIG. 5. *H. misippus*, ♂. Durban. Figured to show the wide difference between the ♂ and its mimetic ♀.)

FIG. 11. *Pseudacraea poggei*, Dew. ♀. Johnstone Falls, North-East Rhodesia. The sexes are similar but the ♂ is smaller.

FIG. 13. *Argynnis hyperbius*, Linn. ♀. Occurs in Abyssinia. The ♂ is without the white sub-apical bar.

FIG. 15. *Diestogyna iris*, Auriv. ♀. Lake Bangweolo. From an example in the Hope Department.

(FIG. 14. *D. iris*, ♂, from the same locality. From an example in the Hope Department. Figured to show the extreme sexual dimorphism.)

FIG. 6. *H. misippus*, f. *alcippoides*, Butl. ♀. An example from German East Africa.

FIG. 10. *H. misippus*, f. *inaria*, Cram. ♀. An East African example. The trace of the formerly existing white sub-apical bar is quite distinctly outlined.

FIG. 12. *H. misippus*, f. *inaria*, ♀. From an example in the Hope Department. One of fifty ♀♀ bred by Mr. Rogers from an intermediate ♀ very similar to Fig. 16.

FIG. 16. *H. misippus*, ♀. Dar-es-Salaam. An intermediate variety showing a transition between *inaria* and *alcippoides*.

D. alcyon

D. alcyon

D. alcyon

D. alcyon

D. alcyon

D. alcyon

D. alcyon

D. alcyon

D. alcyon

D. alcyon

D. alcyon

D. alcyon

Arg. hyperantus

D. alcyon

D. alcyon

D. alcyon

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PLATE III

MODELS.

THE FORMS OF *D. chrysippus* ON PLATE II.
chrysippus chrysippus.

(*chrysippus*, *f. dorippus*.)

(*chrysippus*, *f. alcippus*.)

FIG. 11. *Aletis helcita*, Clerck. Gaboon.

FIG. 9. *Phaegorista agaristoides*, Boisd. Sierra Leone.

FIG. 16. *Acraea alciope*, Hew. ♂. Cameroon. The ♂ is the same throughout the range of the species. The ♀ adopts the appearance of at least two models.

FIG. 17. *Planema macaria*, Fabr. ♂. Sierra Leone. The discal area of the hind-wing upperside is slightly paler in the figure than in the original example.

FIG. 19. *Planema godmani*, Butl. ♂. Sierra Leone. From an example in the Hope Department.

FIG. 21. *Acraea sotikensis*, E. M. Sharpe, ♂. Kisumu, British East Africa. From an example in the Hope Department. The sexes are similar.

(*Amauris echeria*, Plate V.)

(*D. chrysippus*, *f. dorippus*, Plate II.)

FIG. 27. *Planema latifasciata*, E. M. Sharpe, ♂. Toro, West Uganda. From an example in the Hope Department. The sexes are probably similar.

MIMICS.

FIG. 1. *Acraea encedon*, Linn. ♂. Natal. The sexes are similar.

FIG. 4. *Acraea wigginsi*, Neave, ♀. From the type in the Hope Department. North-east shore of Lake Victoria Nyanza. The sexes are similar.

FIG. 5. *Acraea mima*, Neave, ♂. North-East Rhodesia. From an example in the South Kensington Museum. The ♀ is duller in colour. (See text.)

FIG. 6. *Mimacraea marshalli*, Trim. ♂. Lualaba Valley. The sexes are similar.

FIG. 8. *Cooksonia trimeni*, Druce, ♀. North-East Rhodesia. Copied by kind permission from Mr. Druce's figure in Trans. Ent. Soc., 1905.

FIG. 2. *Acraea encedon*, *f. दौरa*, Godm. ♀. Dar-es-Salaam. The example figured is usually large. The trace of the white sub-apical bar is still faintly discernible.

FIG. 7. *Mimacraea marshalli*, *f. doherlyi*, R. and J., ♂. Kikuyu Escarpment. From an example in the Hope Department. The trace of the white bar of *marshalli* is only just discernible.

FIG. 3. *Acraea encedon*, *f. alcippina*, Auriv. ♂. Sierra Leone. Examples from this region are frequently much larger than the figure. The model is especially abundant on the west coast.

FIG. 12. *Euphaedra ruspina*, Hew. ♀. Gaboon. The ♂ is smaller and has the ground-colour rather paler.

FIG. 13. *Telipna sanguinea*, Plötz. West Africa. The sexes are similar.

FIG. 14. *Pseudaletis agrippina*, Druce, ♀. Lagos. From an example in the South Kensington Museum. The specimen is rather worn, and probably presented a richer coloration during life. The sexes do not appear to present important differences.

FIG. 15. *Euptera (Cymothoe) crowleyi*, Smith and Kirby, ♀. Ogowe. From an example in the South Kensington Museum. Probably a mimic of a yellow form of *Aletis*. (See text.)

FIG. 10. *Euphaedra eusemoides*, Smith and Kirby, ♀. Sierra Leone. The example figured was received in the same collection with the moth shown at Fig. 9.

FIG. 20. *Mimacraea fulvaria*, Auriv. ♀. Congo region, West Coast. Copied by kind permission from the figure in 'Rhopalocera Aethiopica'.

FIG. 29. *Elymnias phegea*, Fabr. Sierra Leone. From an example in the Hope Department. The sexes are similar, but the colouring of the species varies, and there are varieties mimicking at least two other models. See Plates VII and VIII. The example here figured presents a definite approach to the *alciope* type of coloration.

FIG. 18. *Mimacraea fulvaria*, ♂ (?). Sierra Leone. From an example in the Hope Department. Though the upperside bears a generally Planemoid appearance, it is on the underside that the mimicry of *Planema* is most remarkable.

FIG. 23. *Acraea alciope*, ♀. Sierra Leone. From an example in the Hope Department. The specimen is typical of the West African form of *alciope* ♀, and mimics the corresponding forms of *Planema*. The East African *alciope* ♀ resembles an entirely different *Planema*. See Plate VIII.

FIG. 22. *Mimacraea poulloni*, Neave, ♂. Kisumu, British East Africa. From the type in the Hope Department. The upperside colouring is variable. (See text.)

FIGS. 24 and 25. *Acraea lycoa fallax*, Godm. ♀ and ♂. Kilimanjaro. From examples in the Hope Department.

FIG. 26. *Acraea johnstoni*, *f. fulvescens*, Oberth. ♂. Kilimanjaro. From an example in the Hope Department.

FIG. 28. *Acraea johnstoni toruna*, Smith and Kirby, ♂. From an example in the Hope Department. The sexes are similar.

A. encadatus ♂ 1

M. mandata ♂ 2

A. encadatus ♀ 3

A. encadatus ♀ 4

A. encadatus ♀ 5

M. mandata ♂ 6

M. mandata ♂ 7

A. encadatus ♀ 8

A. encadatus ♀ 9

E. encadatus ♀ 10

A. helbta 11

12

13

14

15

16

A. alceps ♂

17

18

19

20

21

22

23

24

A. lyssa fallax ♂

25

A. lyssa fallax ♂

26

A. lyssa fallax ♂

27

A. lyssa fallax ♂

28

A. lyssa fallax ♂

29

A. lyssa fallax ♂

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PLATE IV

MODELS.

FIG. 1. *Melinda formosa*, Godm. ♂. Dar-es-Salaam.

FIG. 2. *Melinda formosa*, ♀. British East Africa. From an example in the Hope Department.

(The ground colour of both these figures should be darker.)

FIG. 3. *Melinda mercedonia*, Karsch, ♂. Entebbe.

FIG. 8. *Tirumala petiverana*, Doubl. ♂. Entebbe.

FIG. 10. *Amauris hyalites*, Butl. ♂. Ogowe.

FIG. 12. *Amauris psyttalea*, Plötz, ♂. Entebbe.

FIG. 13. *Amauris ochlea*, Boisd. ♀. Delagoa Bay.

FIG. 14. *Amauris hecate*, Butl. ♀. Cameroon.

MIMICS.

FIG. 5. *Papilio rex*, Oberth. ♂. Kikuyu Escarpment, British East Africa. From an example in the Hope Department.

FIG. 6. *Papilio rex*, ♀. Kikuyu Escarpment, British East Africa. From an example in the Hope Department.

FIG. 7. An intermediate ♀ form between *rex* and *mimeticus*. Kisumu. From an example in the Hope Department.

FIG. 4. *Papilio mimeticus*, Roths. ♀. German East Africa.

FIG. 9. *Papilio leonidas*, Fabr. ♀. Entebbe.

FIG. 11. *Papilio leonidas*, f. *brasidas*, Feld. ♀. Angola.

FIG. 16. *Aterica galene*, Brown, ♀. Entebbe. In the ♂ the spots are pale yellow.

FIG. 17. *Hypolimnias deceptor*, Trim. ♀. Natal.

FIG. 15. *Pseudacraea lucretia*, f. *expansa*, Butl. ♂. Delagoa Bay.

FIG. 18. *Hypolimnias dubius*, form *damoclina*, Trim. ♀. Cameroon. The example is somewhat unusual in having yellow in the hind-wing. The pale area is generally white, thus accentuating the resemblance to *Amauris*.

FIG. 19. *Melinda morgeni*, Honr. ♂. Bipindi, Cameroon. From an example in the Tring Museum. The generally *Amauris*-like pattern is very striking and comes perhaps nearest to *A. hecate*.

1. *M. formosa* ♂ 2. *M. formosa* ♀ 3. *M. mercedonia* ♂ 4. *P. mimeticus* ♂ 5. *P. rex* ♂ 6. *P. rex* ♀

7. Intermediate form ♀

8. *T. petiverana* ♂ 9. *P. leonidas* ♀ 10. *A. hyalites* ♂ 11. *P. leonidas* f. *brasidas* ♀ 12. *A. psytalea* ♂ 13. *A. ochlea* ♀ 14. *A. hecate* ♀ 15. *Ps. lucretia*
f. *expansa* ♂ 16. *A. galene* ♀ 17. *H. deceptor* ♀ 18. *H. dubius* var. *damoclinus* 19. *M. morgeni* ♂

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PLATE V

MODELS.

FIG. 1. *Amauris niavius dominicanus*, Trim. ♂. Natal.

FIG. 2. *Amauris niavius*, Linn. ♂. Sierra Leone.

FIG. 3. *Amauris psyttalea*, f. *damocliides*, Staud. ♂. German East Africa.

FIG. 4. *Amauris albimaculata*, Butl. ♂. Durban. From an example in the Hope Department.

FIG. 10. *Amauris echeria*, Stoll, ♂. German East Africa. A brown variety. (See text.)

FIG. 13. *Amauris echeria*, f. *jacksoni*, E. M. Sharpe, ♂. Kilimanjaro. From an example in the Hope Department.

FIG. 16. *Planema paragea*, Smith and Kirby, ♂. Entebbe.

FIG. 18. *Planema consanguinea*, Auriv. ♂. Gold Coast. The specimen here shown, though not identical with the type *consanguinea*, agrees more closely with it than with any other form with which I have had an opportunity of comparing it.

MIMICS.

FIG. 5. *Hypolimnias dubius*, f. *wahlbergi*. Wallengr. Natal (= *Euralia wahlbergi*, auct.).

FIG. 9. *Hypolimnias usambara*, Ward, ♂. Mombasa. From an example in the Hope Department.

FIG. 6. *Hypolimnias dubius*, f. *anthedon*, Doubl. ♀. Sierra Leone.

FIG. 7. *Papilio echerioides*, Trim. ♀. Dar-es-Salaam. The ♂ is very different in appearance. (See text.)

FIG. 15. *Hypolimnias dubius dubius*, Beauv. ♂. Dar-es-Salaam.

FIG. 8. *Papilio jacksoni*, E. M. Sharpe, ♀. Uganda. The ♂ is very different in appearance. (See text.)

FIG. 12. *Hypolimnias dubius*, f. *mima*, Trim. ♀. Natal.

FIG. 11. *Papilio homeyeri*, Plötz, ♀. The male is very different in appearance. (See text.)

FIG. 14. *Pseudacraea lucretia*, f. *tarquinia*, Trim. ♀. Natal. A peculiar variety. The spots on the fore-wing are usually more distinct, giving a close resemblance to the type form of *echeria*. (See text.)

FIG. 17. *Papilio cynorta*, f. *peculiaris*, Neave, ♀. Entebbe. From an example in the Grist Collection, by kind permission of Mr. C. J. Grist.

FIG. 19. *Pseudacraea fulvaria*, Butl. ♂ (?). Gold Coast. The identity of this specimen is rather doubtful. (See text.)

1. *A. niavius dominicanus* ♂ 2. *A. niavius* ♂. 3. *A. psittalea*
f. damocles ♂. 4. *A. albimaculata* ♂. 5. *H. dubius*
f. wahlbergi ♀ 6. *H. dubius f. anthedon* ♀ 7. *P. echerioides* ♀ 8. *P. jacksoni* ♀ 9. *H. usambara* ♂ 10. *A. echeria* ♂ 11. *P. homeyeri* ♀ 12. *H. dubius f. mima* ♀ 13. *A. echeria f. jacksoni* ♂ 14. *Ps. lucretia f. tarquinia* ♀ 15. *H. dubius*. 16. *Pl. paragea* ♂
H. Eltringham del. 17. *P. cynorta* ♀, *f. peculiaris*. 18. *Pl. consanguinea* ♂ 19. *Pl. fulvaria* ♂ (?)

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PLATE VI

MODELS.

FIG. 1. *Acraea egina*, Cram. ♂. Entebbe. Also occurs as far north and west as Sierra Leone.

FIG. 2. *Acraea egina*, ♀. Sierra Leone.

FIG. 3. *Acraea zetes acara*, Hew. ♂. Natal. The example figured is below the average in size.

FIG. 6. *Acraea zetes acara*, ♀. Chirinda. From an example in the Hope Department.

FIG. 11. *Acraea orina*, Hew. ♂. Sesse Island, Victoria Nyanza. Extends also to West Africa. The sexes are similar.

FIG. 12. *Crenis pechueli*, Dewitz, ♂. Alala Plateau, North-West Rhodesia. From an example in the Hope Department.

FIG. 13. *Planema vestalis*, Feld. ♀. Sierra Leone. Both sexes are rather variable in depth and brilliancy of colour.

MIMICS.

FIG. 4. *Pseudacraea boisduvali*, Doubl. ♂. Raketta River, Freetown.

FIG. 7. *Papilio ridleyanus*, White, ♂. Entebbe. The sexes are similar, and the species has a range corresponding to that of *A. egina*.

FIG. 5. *Pseudacraea boisduvali*, ♀. Raketta River. The resemblance to the ♀ *egina* is not so marked as that between the respective ♂♂. (See text.)

FIG. 10. *Pseudacraea boisduvali trimeni*, Butl. ♂. Natal. An example of the white suffused form.

FIG. 8. *Pseudacraea boisduvali trimeni*, ♂. Natal. A richly-coloured example lacking the white suffusion.

FIG. 9. *Pseudacraea boisduvali trimeni*, ♀. Chirinda. From an example in the Hope Department. The white suffusion is of a crude and chalky appearance in this specimen. As in the model, this feature is variable.

FIG. 14. *Pseudacraea clarki*, Butl. ♂. Though particularly resembling *orina*, both species may be considered as synposematic with *egina*.

FIG. 15. *Crenidomimas concordia*, Hopff. ♂. Mporokoso, North-East Rhodesia. From an example in the Hope Department. The ♀♀ of both model and mimic are darker, and show perhaps a still closer resemblance.

FIG. 16. *Pseudacraea striata*, Butl. ♀. Sierra Leone.

1. *A. egina* ♂

2. *A. egina* ♀

3. *A. zetes acara* ♂

4. *Ps. boisduvali* ♂

5. *Ps. boisduvali* ♀

6. *A. zetes acara* ♀

7. *P. ridleyanus* ♂

8. *Ps. boisduvali trimeni* ♂

9. *Ps. boisduvali trimeni* ♀

10. *Ps. boisduvali trimeni* ♂

11. *A. orina* ♂

12. *C. pechueli* ♂

13. *Pl. vestalis* ♀

14. *Ps. clarki* ♂

15. *Cr. concordia* ♂

16. *Ps. striata* ♀

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PLATE VII

MODELS.

FIG. 1. *Planema epaea*, Cram. ♂. Sierra Leone.

FIG. 2. *Planema epaea*, ♀. Sierra Leone.

FIG. 3. *Planema macarista*, Sharpe, ♀. Entebbe.
The ♂ is figured on Plate VIII.

(*Planema aganice*, Hew.)

(*Planema aganice*, f. *montana*, Butl. ♂.)

(*Planema aganice*, f. *montana*, ♀.)

FIG. 10. *Planema elongata*, Butl. ♀. Ogowe.
The ♂ is darker.

FIG. 12. *Atella phalantha*, Drury, ♂. Widely distributed over Africa and also found in Asia. The ♀♀ are often darker.

MIMICS.

FIG. 4. *Pseudacraea eurytus*, Linn. ♂. Sierra Leone.

FIG. 5. *Pseudacraea eurytus*, ♀. Sierra Leone. The sexual dimorphism of the model is copied by the mimic. The underside mimicry is especially well developed in the ♀.

FIG. 8. *Papilio cynorta*, Fabr. ♀. Accra. The ♂ is very different in appearance. (See text.)

FIG. 9. *Elymnias phegea*, Fabr. Sierra Leone. The sexes are similar. The black and white form mimics *Planema epaea* in the west and *P. alcinoe* ♀ and *P. macarista* ♀ in the east.

FIG. 6. *Pseudacraea hobleyi*, Neave, ♀. Entebbe. The ♂ has a yellow bar on the fore-wing. (See Plate VIII.)

FIG. 7. *Pseudacraea imitator*, Trim. ♀. Natal. From an example in the Hope Department. The ♂ is similar in appearance.

FIG. 11. *Pseudacraea rogersi*, Trim. ♂. Mombasa. From the type in the Hope Department.

FIG. 14. *Pseudacraea rogersi*, ♀. Mombasa. From the type in the Hope Department.

FIG. 13. *Pseudacraea ruhamia*, Hew. ♀. Ogowe. The ♂ differs in a manner corresponding to the ♂ *Pl. elongata*.

FIG. 15. *Pseudargynnis hegemone*, Godt. ♂. Sierra Leone. Also extending to Mount Ruwenzori. The ♀♀ are often darker, as in the model.

1. *Pl. epaea* ♂ 2. *Pl. epaea* ♀ 3. *Pl. macarista* ♀ 4. *Ps. eurytus* ♂ 5. *Ps. eurytus* ♀ 6. *Ps. hobleii* ♀ 7. *Ps. imitator* ♀ 8. *P. cynorta* ♀ 9. *E. phegea*. 10. *Pl. elongata* ♀ 11. *Ps. rogersi* ♂ 12. *A. phalantha* ♂ 13. *Ps. ruhami* ♀ 14. *Ps. rogersi* ♀ 15. *Psrg. hegemon* ♂

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PLATE VIII

MODELS.

FIG. 1. *Planema macarista*, Sharpe, ♂. Entebbe. The ♀ is figured on Plate VII.

FIG. 2. *Planema poggei*, Dewitz, ♀. Entebbe. The ♂ is similar but has narrower wings.

FIG. 3. *Planema tellus*, Auriv. ♀. Cameroon. Also occurs at Entebbe. The ♂ is similar, but has somewhat narrower wings.

FIG. 14. *Acraea oberthüri*, Butl. ♂. Cameroon. The ♀ is somewhat paler.

MIMICS.

FIG. 4. *Acraea alciope*, ♀ form *aurivillii*. Entebbe. (See text.) From an example in the Hope Department.

FIGS. 5 and 7. *Pseudacraea künowi*, Dewitz, ♂ and ♀. Sesse Island, Victoria Nyanza.

FIG. 8. *Pseudacraea hobleyi*, Neave, ♂. Entebbe. The ♀ is black and white. (See Plate VII.)

FIG. 11. *Precis rauana*, Grose Smith, ♂. Entebbe. From an example in the Hope Department. The ♂ is without the white suffusion in the hind-wing.

FIG. 10. *Elymnias phegea*, Fabr. Toro, Uganda. From an example in the Hope Department. (See also Plates III and VII.)

FIG. 13. *Acraea johnstoni*, f. *semifulvescens*, Oberth. ♀. Taveta. From an example in the Hope Department.

FIG. 6. *Pseudacraea terra*, Neave, ♂. Entebbe. The ♀♀ are similar in appearance.

FIG. 9. *Acraea jodutta*, Fabr. ♀. Entebbe. From an example in the Hope Department. In the ♂ the markings are pale ochreous.

FIG. 12. *Acraea althoffi*, Dewitz, ♀. Entebbe. From an example in the Hope Department. There are several forms of ♀ in this species. (See text.)

FIG. 17. *Mimacraea darwinia*, f. *apicalis*, Smith and Kirby. Cameroon. The general effect of the pattern gives a marked resemblance to the *tellus* group.

FIG. 16. *Acraea encedon*, ♀ variety. Nyangori, North-East Victoria Nyanza. From an example in the Hope Department. There is a distinct approach towards the *tellus* type, caused by the yellow suffusion of the sub-apical bar.

FIG. 15. *Mimacraea neavei*, Eltr. Cameroon. From the type now in the Hope Department. The only example at present known. Owing to slight damage the sex is undetermined (probably ♀).

1. *Pl. macarista* ♂

2. *Pl. poggei* ♀

3. *Pl. tellus* ♀

4. *A. alciope* ♀

5. *Ps. kunowi* ♀

6. *Ps. terra* ♂

7. *Ps. kunowi* ♂

8. *Ps. hoblely* ♂

9. *A. jodutta* ♀

10. *El. phegea*.

11. *Pr. rauana* ♀

12. *A. althoffi* ♀

13. *A. johnstoni semifulvescens* ♀

14. *A. oberthuri* ♂

17. *M. darwinia apicalis*.

15. *M. neavei*.

16. *A. encedon* ♀

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PLATE IX

MODELS.

FIG. 1. *Mylothris agathina*, Cram. ♂. Underside. Cape.

FIG. 6. *Mylothris spica*, Mösch. ♀. Southern Nigeria.

FIG. 9. *Mylothris agathina*, ♀. Buffalo River.

FIG. 11. *Mylothris asphodelus*, Butl. ♂. Kassai River, Congo.

FIG. 12. *Mylothris trimenia*, Butl. ♂. East London, Cape.

FIG. 13. *Mylothris trimenia*, ♀. East London, Cape.

FIG. 14. *Mylothris spica*, ♂. Sierra Leone.

FIG. 15. *Mylothris poppea*, Cram. ♀. Sierra Leone.

FIG. 21. *Pardopsis punctatissima*, Boisd. ♀. Fort Jameson. The sexes are similar.

FIG. 22. *Terias brigitta*, Cram. ♂. Niger River. The ♀ is paler.

FIG. 23. *Terias senegalensis*, Boisd. ♂. Loangwa River, Portuguese East Africa. The ♀ is rather paler.

FIG. 24. *Leptosia medusa*, Cram. Entebbe. The sexes are similar.

(*Mylothris bernice*, Hew. (See text.))

(With the exception of Figs. 14, 15, 19, and 20, all the illustrations on this plate are from examples in the Hope Department.)

MIMICS.

FIG. 2. *Phrissura phoebe*, Butl. ♀. Underside. North-east shore of Lake Victoria Nyanza.

FIG. 3. *Pinacopteryx rubrobasalis*, Lanz. ♀. Underside. Taita, British East Africa.

FIG. 4. *Belenois thysa*, Hopff. ♂. Underside. Mombasa.

FIG. 5. *Eronia argia*, Fabr. ♀. Underside. Karkloof, Natal.

FIG. 7. *Phrissura sylvia*, Fabr. ♀. Lagos.

FIG. 8. *Eronia thalassina*, Boisd. ♀. West Africa.

FIG. 10. *Belenois thysa*, ♀. Taveta.

FIG. 16. *Phrissura perlucens*, Butl. ♂. Kassai River, Congo.

FIG. 17. *Phrissura lasti*, Grose Smith, ♂. British East Africa.

FIG. 18. *Phrissura lasti*, ♀. British East Africa.

FIG. 19. *Phrissura sylvia*, ♂. Sierra Leone.

FIG. 20. *Phrissura phoebe*, Butl. ♀. Sierra Leone.

FIG. 26. *Pentila amenaida*, Hew. ♀. Fort Jameson. The sexes are similar.

FIG. 27. *Citrinophila similis*, Kirby, ♀. Southern Nigeria. The ♂ has more black on the fore-wings.

FIG. 28. *Liptena homeyeri*, Dewitz. Loangwa River. The sexes are similar.

FIG. 25. *Teriomima xantha*, Grose Smith. Entebbe.

FIG. 29. *Larinopoda tera*, Hew. Entebbe. The sexes are similar.

FIG. 30. *Citrinophila erastus*, Hew. ♀. Kiva, Southern Nigeria. The ♂ is yellower and has a broader black border on the hind-wing.

1. *M. agathina* ♂ 2. *Ph. phoebe* ♀ 3. *Pin. rubrobasalis* ♀ 4. *B. thysa* ♂ 5. *E. argia* ♀ 6. *M. spica* ♀ 7. *Ph. sylvia* ♀ 8. *E. thalassina* ♀ 9. *M. agathina* ♀ 10. *B. thysa* ♀ 11. *M. asphodelus* ♂ 12. *M. trimenia* ♂ 13. *M. trimenia* ♀ 14. *M. spica* ♂ 15. *M. poppea* ♀ 16. *Ph. perlucens* ♂ 17. *Ph. lasti* ♂ 18. *Ph. lasti* ♀ 19. *Ph. sylvia* ♂ 20. *Ph. phoebe* ♀ 21. *Pard. punctatissima*. 22. *T. brigitta*. 23. *T. senegalensis*. 24. *Lep. medusa*. 25. *Ter. xantha*. 26. *Pent. amenaïda*. 27. *Cit. similis*. 28. *L. homeyeri*. 29. *Lar. tera*. 30. *Cit. erastus*.

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PLATE X

MODELS.

MIMICS.

(FIG. 2. *Papilio dardanus cenea*, Stoll, ♂. Mombasa.)

FIG. 1. *P. dardanus meriones*, Feld. ♀. Madagascar. From an example in the Hope Department. Note the black bar extending across the cell in the fore-wing.

FIG. 3. *P. dardanus polytrophus*, ♀ form *trimeni*, Poulton. Kikuyu Escarpment. From the type in the Hope Department. An intermediate form. Note the rudimentary tails in the hind-wing.

FIG. 4. *P. dardanus antinorii*, ♀ form *niavioides*, Kheil. Abyssinia. Copied by kind permission of the publishers from the figure in Haase's 'Researches in Mimicry'.

FIG. 8. *P. dardanus antinorii*, ♀ form *ruspinae*, Kheil. Abyssinia. Copied by kind permission of the publishers from the figure in Haase's 'Researches in Mimicry'.

(*Amauris niavius*)

FIG. 5. *P. dardanus*, ♀ *hippocoön*, Fabr. Gaboon. From an example in the South Kensington Museum. This specimen is especially interesting as showing the rudimentary tails in the hind-wings.

(*Amauris niavius*
dominicanus)

FIG. 6. *P. dardanus cenea*, ♀ form *hippocoön*, Fabr. Mombasa. The black border of the hind-wing is distinctly narrower, corresponding to that in the model.

FIG. 7. *P. dardanus*, ♀ form *dionysos*, Doubl. From a West African example in the Hope Department. Represents an intermediate variety between *hippocoön* and *trophonius*.

(*D. chrysippus*.)

FIG. 9. *P. dardanus*, ♀ form *trophonius*, Westw. Victoria Nyanza. From an example in the Hope Department. The western form of this variety exhibiting the dark internervular rays in the hind-wing.

FIG. 10. *P. dardanus cenea*, ♀ form *trophonius*. Natal. From an example in the Hope Department. The specimen is one of the offspring of a *trophonius* ♀, from the eggs of which Mr. Leigh bred six ♂♂ and seven ♀♀. Of the latter only this individual is *trophonius*, the rest being all of the *cenea* form.

(*D. chrysippus*,
f. dorippus.)

FIG. 11. *P. dardanus tibullus*, ♀ form *dorippoides*, Trim. Nairobi. From an example in the Hope Department.

(*Planema poggei*.)

FIG. 12. *P. dardanus*, ♀ form *planemoides*, Trim. Kisumu. From an example in the Hope Department.

(*Amauris ccheria*.)

FIG. 13. *P. dardanus cenea*, ♀ form *cenea*, Stoll. Natal. From an example in the Hope Department. The example is one of the offspring of a ♀ *cenea* form which produced fifteen ♂♂, sixteen ♀♀ of the *cenea* form, and one ♂ *hippocoön*. (See text.)

FIG. 14. *P. dardanus cenea*, ♀ form *cenea*. Durban. White-spotted form.

FIG. 15. *P. dardanus polytrophus*, ♀ form *trimeni cenea*. Kikuyu Escarpment. From an example in the Hope Department.

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