

MIMICRY IN NORTH AMERICAN BUTTERFLIES: A REPLY.

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Certain criticisms of the theories of mimicry and warning colors have recently appeared in the publications of The Academy of Natural Sciences of Philadelphia, and it is, I think, a convenience that the controversy should be continued in the same channel. The occasion also enables me to contribute in, I hope, an appropriate way to the publications of the great and learned society with which I have the honor and pleasure of being specially associated.

In the present paper I propose to deal with the friendly criticisms contained in Dr. Henry Skinner's paper (32). It will be most convenient, I think, to consider the author's arguments under separate heads, which I have arranged as far as possible in the same order as that adopted in his memoir.

1. THE ATTACKS OF BIRDS ON BUTTERFLIES AND THE THEORIES OF MIMICRY.

The believers in these theories, both Batesian and Müllerian, will cordially agree with Dr. Skinner as to the paramount importance

of showing "that birds are in the habit of eating butterflies and that some butterflies are poisonous or nauseous to them and others not." (32, p. 121.) It must be admitted also that we require vastly more evidence than we at present possess. But evidence is accumulating steadily, and some of the best has been forthcoming in recent years. I may refer especially to Mr. S. A. Neave's observation (30) on January 12, 1912, of a Wagtail devouring Lycænid and Pierine butterflies, but rejecting an *Acraea*, in the bed of a forest stream near Entebbe, Uganda.

Dr. Skinner, in a more recent paper (34, p. 25) refers to the fact that the Biological Survey of the United States examined fifty thousand bird stomachs and only found butterflies in five of them. Mr. C. F. M. Swynnerton has quite lately thrown much light on this method of investigation (33). He is convinced, as the result of recent work at Chirinda, Gazaland, southeast Rhodesia, "that conclusions based on stomach-examination are likely to be fallacious, unless that examination has been so thorough and minute that even such small objects as the scales of Lepidoptera must have been detected if present, even in small numbers, in either stomach *or* intestines, unless a very large series has been so examined for each species, and unless, finally, a note had been made at the time of the shooting of each specimen as to the probable proportions in which insects of various kinds were present at the moment." Mr. Swynnerton's paper was especially intended as a reply to Mr. G. L. Bates (25), whose statements are quoted by Dr. Skinner (32, p. 122). I have treated this subject very briefly and inadequately because I hope to return to it in a later paper dealing with the attacks made by Mr. W. L. McAtee in a memoir (28) written in a very different spirit from that of Dr. Skinner.

2. HAASE'S NAME "PHARMACOPHAGUS" AND HIS HYPOTHESIS THAT MIMICKED BUTTERFLIES (MODELS) DERIVE NAUSEOUS QUALITIES FROM THE LARVAL FOOD-PLANTS.

Dr. Skinner, influenced by my use of Haase's term "*Pharmacophagus*," is apparently under the impression that I am a convinced follower of his hypothesis. This is by no means the case. In a review (14) of Haase's work (13) I expressed the opinion, to which I still adhere, that the hypothesis is probably true—although as yet quite unproved—for some distasteful species, but that it is certainly not true of others. Rothschild and Jordan (20, 433-4), following Horsfield (1) and Haase (9), have shown that the *Papilioninæ* are

divisible into three well-marked sections differing in larval, pupal and imaginal characters. They give descriptive titles to each of the sections, but do not suggest names which can be used at any rate provisionally as genera. In the meantime, it is highly inconvenient to include in the genus *Papilio* the species of all three groups. For this reason, and for this reason alone, I provisionally adopted Haase's *Pharmacophagus* for the "Aristolochia swallowtails," his *Papilio* for the "Fluted swallowtails," and his *Cosmodesmus* for the "Kite swallowtails."

I am quite ready to abandon any or all of these when it is proved that the three groups may be referred to by other names with a prior claim, and, under any circumstances, Haase's terms cannot, with their present meaning, permanently stand for genera, because, as I learn from Dr. Jordan, each of the three sections is a much larger group which must itself be split up into genera. Furthermore, I do not, as Dr. Skinner states on p. 124, accept any conclusions or use any argument based on the meaning of the word when I provisionally employ "*Pharmacophagus*" as the name of a genus of the Papilios, and I do not think that any words of mine can be quoted which will bear out Dr. Skinner's interpretation.

Inasmuch as Haase's hypothesis occupies so large a place in Dr. Skinner's memoir, I venture to offer a few remarks upon the idea itself as well as upon some of the author's criticisms.

The great majority of the pigments possessed by plant-eating insects are built up in the laboratory of the living organism, in spite of the fact that the larval food is rich in chlorophyll. Nevertheless, this color exists ready-made, and certain insects have been specially adapted to avail themselves of it and thus to gain certain pigments. I proved this many years ago by spectroscopic examination as well as in other ways (3, 4), including experiments in which larvæ were fed upon parts of leaves devoid of chlorophyll (10)—experiments recently repeated with confirmatory results upon different species by Prof. W. Garstang (24). I think it probable that nauseous or poisonous substances, when they exist in a plant or in a group of allied plants, may be employed by certain species which are restricted to it or them; but as yet the proof is wanting. Among the most probable instances, and those which should first be tested by chemical means, are the *Danainæ* feeding on the Asclepiads and the "*Pharmacophagus*" swallowtails feeding on *Aristolochia* and its allies. I may here remark that Dr. Skinner is mistaken in supposing that Haase in his hypothesis drew any distinction between the *Danainæ* and the

section of the Papilios to which he gave the name *Pharmacophagus*. He maintained that both of them, and the *Ithomiinæ* and *Acræinæ* as well, derived their distasteful qualities direct from the larval food-plants. I refer to the following passage in which Dr. Skinner is speaking of *Danaida plexippus* (32, p. 126):

“The protective idea in this case is the same as in the so-called pharmacophagus butterfly, the imago of *plexippus* which is said to be repugnant to birds but the repugance is not based on the idea of the butterfly feeding on a poisonous plant (*Asclepias*) in the larval stage.”

As regards the specially protected and much-mimicked group of the *Acræinæ*, the recent hitherto unpublished researches of my friend Mr. W. A. Lamborn upon their larvæ in the Lagos district strongly suggest that the butterflies do not derive the nauseous qualities, which they undoubtedly possess, in the manner assumed by Haase; for the food-plants belong to varied groups. In a letter written July 16, 1913, and received as I am preparing this paper, Mr. Lamborn states: “By far the most common *Acræa* here [the neighborhood of Ibadan, S. Nigeria, W. Africa] is *terpsichore*. Its larvæ abound, and seem, like so many other distasteful caterpillars, to have a wide range of food-plants.”

The facts brought forward by Dr. Skinner do not appear to me to affect the probability of Haase's hypothesis. It is well known that insects feeding on a great variety of plants commonly include among these species with poisonous qualities. Haase's hypothesis only refers to certain insects *confined to* poisonous or acrid food-plants. I say “certain” insects, for the power of utilizing the poisonous quality, if it exist at all, is undoubtedly a special adaptation by no means necessarily present in any larva which feeds on the plant possessing the quality. The other fact alluded to by the author, that the acrid principle may be present in very small quantity, is, I think, equally devoid of bearing on the hypothesis. If the adaptation exist at all, we should expect small quantities to be stored up and concentrated. The percentage of lime in a leaf is very small, yet the larva of *Clisiocampa neustria* reserves enough to render its cocoon opaque with minute crystals of the carbonate in the form of aragonite (5) and *Eriogaster lanestris* enough to make its eggshell-like cocoon out of the oxalate (8).

Haase's hypothesis cannot be proved or disproved by discussion. It is the work of the chemist that is needed. The most appropriate field in the world for this work is North America with its hundreds

of skilled chemists and its well-equipped laboratories, and with two abundant species—*Danaida (Anosia) plexippus* feeding on Asclepiads and *Pharmacophagus (Papilio) philenor* feeding on Aristolochias—by which to test the validity of Haase's hypothesis.

3. INDIRECT EVIDENCE THAT PHARMACOPHAGUS PHILENOR IS A MODEL POSSESSING DISTASTEFUL QUALITIES.

I have myself only seen this insect alive on one or two occasions, and have certainly never had the opportunity of observing it in relation to its natural enemies, nor do I know of any such observations. Scudder states (6, 1248-9) that the larvæ are gregarious when young and semigregarious in later life, that the perfect insect is very tenacious of life, and he quotes Edwards for the observation that it has a strong and disagreeable scent. These qualities, especially the two latter, are generally characteristic of distasteful species; but Skinner states (32, p. 124) that later specially directed observations have failed to confirm Edwards. Skinner also records (p. 125) the fact that the larvæ are attacked by parasites, but this is commonly true of *Danainæ*, *Acræinæ*, and other distasteful much-mimicked groups. Haase is, so far as I am aware, the only writer on the subject who has supposed that the immunity of models is complete, and probably in all cases protection from insectivorous vertebrates is to a large extent balanced by exceptional exposure to the attacks of parasites and certain other insect enemies, such as Asilid flies and Hemiptera (19).

I quite agree with Skinner (p. 125) that the principal attacks are made during the earlier stages of an insect's life—and think of the elaborate protective adaptations which are common in these stages—yet I do not doubt that the imago is subject to severe persecution from enemies of many kinds. Furthermore, it must be remembered that each imago, the heir of all the other stages, and especially each female, is of far greater value to the species than a single pupa or larva and often hundreds of times as valuable as an ovum.

Although I must admit that there is no direct evidence to prove that *P. philenor* is nauseous to birds (p. 123), I believe that much might be learned if American naturalists would offer large numbers of this swallowtail to many species of insectivorous birds in confinement, offering at the same time other butterflies with a procryptic under-surface, such as *Vanessa milberti* or species of *Grapta (Eugonia)*. The North American Danaine models might be tested at the same time. Although the records of field observations are greatly to be

preferred to this method of experiment, yet in the absence of such observation much may be learned by comparing the behavior of the same individual bird with different species of insects.

The indirect evidence that *Ph. philenor* acts as a model and possesses the qualities of a model seems to me extremely strong. On this hypothesis many facts receive their interpretation; without it they are unexplained and meaningless. *Philenor* is one of the "Aristolochia swallowtails," a section which is abundantly represented in tropical America and in the Oriental Region, but, with the exception of *Ph. antenor* in Madagascar, absent from the Ethiopian Region. The mimicry we observe in North America is not only repeated in both Regions where these swallowtails are abundant, but repeated in a more convincing manner, because the patterns are often far more elaborate, and because an "Aristolochia swallowtail" may break up into numerous geographical races with distinctly different patterns which are mimicked in each locality by corresponding races of the "Fluted swallowtails" and, in the Neotropical Region, of the "Kite swallowtails." A good example is the Oriental *Ph. aristolochiae* with its subspecies mimicked by the females of *Pap. polytes*. Furthermore, there is in this case experimental evidence that *aristolochiae* is distasteful, and its slower, more flaunting flight has often been remarked upon. In the Oriental Region species of *Pharmacophagus* are also sometimes mimicked by day-flying moths, and, in the Neotropical Region, not only by these, but by "Kite swallowtails" (*Cosmodesmus*) and Pierines. Throughout the whole range, as in North America, the mimicking "Fluted swallowtails" are as a rule females, while on the other hand the "Kite swallowtails" are mimetic in both sexes (23). Just as the other much-mimicked groups—the *Danainæ*, *Ithomiinæ*, *Heliconinæ*, and *Acræinæ*—are themselves specially subject to mimicry—the genera or sections of the same subfamily superficially resembling each other and also resembling those of the other subfamilies—so is it in both respects with the South American "Aristolochia swallowtails." In every way these butterflies behave like the great distasteful groups supplying the best known models for mimicry. If we had no experimental or other evidence that the *Danainæ* are unpalatable, the indirect evidence is strong enough to warrant at any rate a provisional acceptance of the hypothesis that they possess some peculiar means of defence which renders them specially advantageous as models. For wherever they are indigenous in the Old World they are mimicked by butterflies of other groups, and even in North America, where

there are only three forms, each one of them is mimicked. It is not as if the models for mimicry were distributed indiscriminately among the butterflies. They are furnished by a few genera here and there among the *Nymphalinae*, *Pierinae*, etc., but the vast majority of them are concentrated in the four subfamilies mentioned above and in the "Aristolochia swallowtails." Until these remarkable and very numerous facts are explained by some other hypothesis or until something stronger than negative evidence is forthcoming, we are justified in accepting the hypothesis of advantageous resemblance to a specially defended model. I should be the last to rest content with indirect evidence, however strong, and for many years I have urged naturalists, and especially those in the tropics, to make observations and to undertake experiments. As a result of much work, a considerable body of direct evidence, which cannot be ignored by any fair-minded opponent, has been steadily accumulating, especially from Africa; but I freely admit that more is greatly needed, and I shall continue to urge my friends to seek for it.

4. THE ATTEMPT TO EXPLAIN MIMETIC RESEMBLANCE AS DUE TO AFFINITY BETWEEN MODEL AND MIMIC.

Dr. Skinner appears to adopt the above interpretation of the likeness between the *Papilios* and *Pharmacophagus* when he says "The three species, *glaucus*, *asterius*, and *troilus*, do bear a resemblance to *philenor* but this happens in any aggregation of species in a genus." (32, p. 125.) This interpretation does not bear inspection. In the first place, the butterflies do not in any real sense belong to the same genus, and it is for this very reason that I have provisionally adopted Haase's *Pharmacophagus* for *philenor*. In the second place, the three mimetic species are placed by Rothschild and Jordan in three different groups of the section "*Papilio*" ("Fluted swallowtails"). In the third place, it is clear that the true affinity is shown by the non-mimetic patterns rather than by the mimetic ones—by the upper surface of the male *asterius* and by the males and *glaucus* females of *glaucus*.

Darwin suggested that mimicry began "long ago between forms not widely dissimilar in color," and Scudder adopts the same hypothesis in the following passage:

"The process has been a long one, so that . . . , we may readily presume far less difference between mocker and mocked when the mimicry between them first began, than now exists between the mocked and the normal relatives of the mocker." (6, p. 715). It is

obvious that this interpretation of the resemblances borne by other insects to the stinging Hymenoptera cannot be thus explained, and, within the Lepidoptera themselves, the study of detail has often furnished a refutation. Thus Prof. Gowland Hopkins (12, p. 680) writes: "The mimicking Pierid retains the characteristic pigments of its group, while those of the mimicked Heliconid are quite distinct. This would seem wholly to refute the argument that in such cases the likeness may spring from a real affinity between the two insects." (See p. 176.)

5. SEXUAL DIMORPHISM (ANTIGENY OF SCUDDER) AND MIMICRY.

The mimetic butterflies of North America, as in other parts of the world, are in large part mimetic in the female sex only, forming a special subsection of the far wider group of sexually dimorphic or antigenetic species. Dr. Skinner seeks to explain the special subsection and the inclusive group by an appeal to the same general law. Thus, speaking of the mimetic females of North American Papilios, he says on p. 125: "These differences [between the sexes] occur in numerous species and it seems logical to consider that they are governed by a general law rather than that a few of them are caused by protective resemblance." He uses the same argument concerning the female *Argynnis diana*, which Scudder maintains in the most positive terms to be a mimic of *Limenitis (B) astyanax*. (6, I, pp. 266, 287, 718; III, p. 1802). Comparing this Argynnid with five other sexually dimorphic species of the genus in North America, Skinner says on p. 126: "It does not seem consistent to pick out one species (*diana*) and say that its antigeny is due to tertiary mimicry. How can the dimorphism of the other species be explained?" But the female *diana* is, according to two eminent North American entomologists, Scudder and Edwards, picked out by nature and distinguished among the other antigenetic females by the fact that it resembles a species of a very different Nymphaline genus. I agree with them—although my opinion is worth very little as compared with theirs, for I have never seen the species alive—and I was seeking to place a resemblance which puzzled Scudder, in its true position among the mimetic butterflies of the Region. The far wider question of sexual dimorphism in general did not fall within the scope of my paper. Again, referring to the mimetic female *Papilio*, I do not know why it is specially logical to seek to explain by the same general law two very different categories, viz., the sexually dimorphic females that closely resemble other species and those that bear no

such resemblance. I doubt whether Dr. Skinner would venture to apply the same argument to the polymorphic mimetic females of the Ethiopian *Papilio dardanus* or to many other examples that could be cited. The North American females are not nearly so striking as these, but their patterns are explained by the theories of mimicry and by no other theories as yet suggested.

There are doubtless certain general principles which underlie the whole phenomenon of sexual dimorphism. One of these is obvious—the linking of color, pattern and structure (as we see in the shape of the wings or in the forefeet of so many butterflies) with sex—a linking which is so apt to occur in insects as well as in several other groups, and is so specially conspicuous in the Lepidoptera Rhopalocera. To this principle I think another may be added, at any rate so far as the butterflies are concerned—the greater variability of sex-limited patterns in the female (23). But these general principles do not explain the different categories of antigenetic females, although they may, and I think do, explain the fact that there is material out of which these categories have been built by selection. They would also, of course, account for any antigenetic characters, if such there be, that have not been subject to selection. They are the nearest approach to a general law governing antigeny as a whole that can be offered in the present state of our knowledge.

Beyond these principles we have, I submit, to look for special explanations rather than for general laws.

(1) The mimetic females are probably to be explained, as Wallace suggested (2, p. 22), by the special needs and special habits of the sex, but also by the fact that the difference in pattern variability may be such that the evolution of mimicry is initiated in one sex and prevented in the other (23, p. 132).

(2) A second class of female patterns is procryptic, meeting the special needs of the sex by promoting concealment.

(3) In a third class the whole or a certain proportion of the females of a species retains ancestral patterns (or structures like the forefeet mentioned above) which have been lost or become more degenerate in the males.

(4) Finally the fact that males are so often distinguished from their females by brilliant tints which are pigmentary in some species and structural in others and by scent-producing organs of many kinds strongly suggests an important fourth class due to the operation of sexual selection.

The summary briefly set forth in the last paragraphs will, I think,

show the hopelessness of any attempt to bring all the examples of sexual dimorphism under any single law except one which expresses the two principles explained on p. 169. The complexity of the subject is still further increased by the fact that different elements in the pattern of a species will often fall into more than one class. Thus Dixey has maintained that the female of *Argynnis diana* belongs to the third of the above classes except as regards "the large expanse of blue ground colour," which is mimetic and belongs to the first class (7, p. 106, footnote).

In his later paper (34) Dr. Skinner has still further developed his objections to any special interpretation of the various classes of sexual dimorphism in butterflies. He speaks of velvety patches on the fore wings of male *Satyrinæ* and brands on the wings of male *Hesperidæ*. The researches of Fritz Müller (29) show that these structures are scent-producing organs, and there is no doubt that they are of use in courtship, or epigamic. The law that would be so comprehensive as to explain at once an epigamic scent-patch, the more rudimentary anterior foot of a male Nymphalid and the mimetic pattern of its female, would be so very general that it would not carry us any distance in the attempt to understand each of these different facts.

Concerning *Papilio glaucus glaucus* and its dark *turnus* female (I adopt Rothschild and Jordan's synonymy, 20, p. 582), which some naturalists at least regard as mimetic of *Ph. philenor*, Skinner says (34, p. 25) in criticism of Edwards: "There is also an assumption to which I take exception. Does anyone know which one [the dark or the male-like female] appeared first and why?" With regard to the last word "why," Edwards had expressly disclaimed knowledge, for he speaks of "some unknown influence" causing the appearance of the black female, and we can say no more than this to-day. With regard to the other part of the question, I think it may be shown that Edwards took the reasonable view in supposing that the dark female appeared later than the male-like one. The male pattern is shown to be ancestral, because it bears an intimate relationship to the pattern of other allied Papilios.

This is the argument used by Scudder (6, p. 534) in the following passage: "In *Jasoniades glaucus*, where we sometimes have a black female, it is more difficult to decide what should be considered the normal color, owing to diversity of view upon the relationship of many of the swallowtails; but, to judge only from those agreed by all to be most nearly allied to it, there can be no question whatever that the striped character prevails."

The *turnus* female is a partially melanic variety, but the lines of the male pattern can be detected beneath the overspreading pigment. It also exhibits many features in its pattern which have received no interpretation except that they are mimetic of *philenor* or secondarily mimetic of the other Papilionine mimics of *philenor* (21, 467-471). No doubt there are examples in which it is probable that melanic females preserve something of an ancestral pattern, as in *Argynnis diana* or the *valesina* form of our British *A. paphia* (7, 103-5, 119-21), but I do not think that anyone has maintained that this is true of the melanic females of Papilios. It is, I submit, unreasonable to suppose that the male-like pattern first appeared almost hidden under the melanism of the *turnus* female, and that the full pattern became evident by the clearing up of the dark pigment; whereas the opposite view, that the partial melanism appeared later, obscuring but not completely hiding a pre-existing male-like pattern, seems to me entirely probable. Such partial melanism, in my opinion, provided the foundation on which the details of the mimetic resemblance were gradually built.

As regard this same species, Dr. Skinner's final conclusions (34, p. 26) are comprised in the following statement: "The evidence in favor of *glaucus* being brought about by mimicry is almost nil, while the evidence against it is very considerable. The species swarms in countless thousands in the north where *glaucus* does not exist." When we add to these last words the fact that the model *P. philenor* is also non-existent in the north, Dr. Skinner's argument seems to support the view he is attacking. *P. philenor* only enters New England and Southern Canada as a straggler and barely overlaps the range of the northern subspecies of *P. glaucus glaucus*, which Rothschild and Jordan distinguish under the name of *P. glaucus canadensis* (20, p. 586). As regards the closely allied *P. rutulus*, the same great authorities give reasons for considering it a distinct species. The whole range of *glaucus glaucus*—Florida to New England and westward to the Mississippi basin—lies within that of *P. philenor*, and over this whole range the dark *turnus* female occurs intermingled with male-like females—the latter preponderating in the north, the former in the south. The evidence based on geographical distribution seems to me strongly to support Edwards' conclusions. And we may add that there are, as I have already said, details in the pattern of the dark females which are not explained by any other hypothesis. Objections based on the great abundance of the non-mimetic ancestor are considered on pages 178, 179.

6. THE FEMALE OF *NEOPHASIA TERLOOTI*, ANOTHER NORTH AMERICAN MIMIC OF *DANAIDA PLEXIPPUS*.

Dr. Skinner remarks (34, p. 27): "What is the cause of the extraordinary antigeny seen in *Neophasia terlooti*? The male in this species is white and the female orange. The female of the species was once sent to me as a 'little *Danais*' and it really looks like one. Here would be a good opportunity to build up a mimicry theory."¹ At the time when I read these words I had never seen the species, but Dr. Skinner has now very kindly sent me a male and female from Reef, Arizona (Nov. 2, 1903: Biederman). There can be no doubt that the female is a mimic of *D. plexippus*. The comparison between the yellow of the under surface exposed in the position of rest and the orange of the upper surface, the blackening of the veins on the upper surface of the hind wing and other details to be described below are quite inexplicable on any other hypothesis. The mimicry is rather rough and there is no approximation in the shape of the wings. In both respects this female stands in about the same position as the females of the Neotropical *Perrhybris* ("*Mylöthris*"). I am greatly indebted to my friend for this opportunity of examining and writing on what is to me an entirely new example of butterfly mimicry in North America—another result of its invasion by the Old World genus *Danaida*. My friend Commander J. J. Walker, who has had an intimate experience of the allied *Neophasia menapia* in Vancouver Island, tells me that during flight the latter is one of the feeblest of Pierines and that it suddenly appears upon the wing in immense numbers. He has kindly permitted me to make use of the following unpublished extracts from his journal, on H. M. S. "Kingfisher" at Esquimalt, Vancouver Island:

1882, August 7: "Day still, hot, and cloudless. During the forenoon I was agreeably surprised by the appearance of a good number of specimens of a very pretty "White" butterfly. . . . It seems to come very near to *Leucophasia*, by the elongate shape and delicate texture of its wings, as well as by the rather short antennæ and hairy palpi. . . . They were flying sluggishly in the sunshine over the water, and the signalman and I caught 15 on the poop in a very short time [the ship being about 300 yards off shore]. . . . Landed at 4 P. M.; the *Leucophasia*? was still on the wing, and I

¹ Dr. F. A. Dixey remarked of *N. terlooti* in 1905 (*Proceedings of the Entomological Society of London*, p. xx): "This latter butterfly is especially interesting as possessing a female which closely resembles some of the mimetic forms of *Euterpe*."

caught 15 or 16 (at flowers of *Matricaria*), all in the most exquisite condition, like those taken on board ship. They all appeared to have emerged from the pupa on that day, as I had been on the lookout for some days past, and certainly did not see one on the wing yesterday."

August 8: "Went on shore this forenoon at 11.30, to get a few more of the *Leucophasia* [*Neophasia*] while it remained in good condition. . . . I had no difficulty in getting as many as I wanted . . . a day, however, had made a perceptible difference in its condition, as a good many were getting somewhat worn and chipped. They were very easy to catch, flitting from flower to flower in the open places [among the pines] and of very weak and sluggish flight."

August 14: The first ♀ was taken on this date. "I beat it out of a fir-tree."

The fact that the only Pierine mimic in the Nearctic Region belongs to a genus with the characteristics described by J. J. Walker suggests an interpretation on the lines of Fritz Müller's hypothesis.

I now propose to institute a detailed comparison between the colored pigments of *Neophasia menapia* and *terlooti*.

THE FEMALE OF NEOPHASIA MENAPIA.—*Under surface of hind wing.*—A colored spot, roughly triangular in shape, is found in the black marginal band of areas 2, 3, 4, 5, and 6. The spots, as well as the other markings described below, were orange in 4 females, orange-red in 2, and a rather pale vermilion in one. The tint in some individuals tends to deepen towards the base of the wing—especially along the costa. Beyond vein 7, viz., in areas 7 and 8, the pigment is continued at first as a narrow marginal line, which filling area 8 except at its very base, broadens with it toward the base of the wing. In the opposite direction, beyond vein 2, area 1c bears two spots, of which the upper is sometimes roughly diamond-shaped. These spots are placed one on each side of the dark line, representing a lost vein, which divides the area longitudinally into two sections. Below vein 1b a narrow marginal orange line extends over about $\frac{1}{3}$ of the breadth of area 1b.

In addition to these marginal orange markings, there is also an internervular development of the same pigment starting from the base of the wing, especially distinct in the lower or inner marginal section of area 1c, which in favorable examples is highly colored over more than half its length starting from the base. In strongly marked females a few scattered orange scales are also seen in area 7 and in the upper section of area 1c, and they could probably be found in other areas of certain individuals.

Upper surface of hind wing. Most of the above-described marginal features appear, but far more faintly, on the upper surface. The other orange marks are not represented on the upper surface of those females that I have examined, nor did they appear anywhere upon either surface of the fore wing.

THE MALE OF NEOPHASIA MENAPIA.—*Under surface of hind wing.*—Sixteen examples were examined and of these about half had a comparatively few dull orange or sometimes yellow scales in one or more of areas 6, 7, and 8. When present they are precisely in the position of the marginal markings of the female.

Since writing the above I have had the opportunity of examining 6 beautiful specimens from Esquimalt, in Commander J. J. Walker's collection. Well-developed marginal markings appeared on all females: on (1) a beautiful cinnabar red; on (2) a pale cinnabar red, a little deepened at the anal angle, apex, and costa; on (3) orange, becoming orange-red in the same positions. Of the 3 males, two possessed pale cinnabar scales at the apex and along the costa, one of them bearing a few at the margin of the upper section of area 1c and still fewer—only 2 or 3 scales—in the lower section. The third male had pale yellow marginal scales at the apex and costa, a few becoming faintly reddish, especially at the apex.

Commander Walker tells me that these butterflies were all "set" immediately after capture, and that they have never been "relaxed" and "reset." Inasmuch as Prof. Gowland Hopkins has shown (11, 12) that the pigments of *Pierinae* are soluble in water, it is probable that Walker's specimens more truly represent the colors of the living insect than do any of the others here described, for all of these have been "relaxed" at least once.

THE MALE OF NEOPHASIA TERLOOTI.—*Under surface of hind wing.*—The marginal markings of the female *menapia* are represented on the male of *terlooti*, smaller indeed, but with a far richer color, being of a bright, rich vermilion tint. In the single specimen I have had the opportunity of examining these markings are solely marginal. They are wanting from area 4 and so slightly developed in all areas except 6, 7, and 8 (where they are purely linear and do not fill the last-named area as in the ♀ *menapia*) that it would be easy to count the constituent scales with a lens. In the specimen before me there are only 3 vermilion scales in area 5 on the left side and only 5 on the right, but they are more numerous and usually far more numerous in all the other markings. Although the dark pigment is comparatively weakly developed in the male, area 1c is divided very

distinctly by a strongly marked linear streak, and the 2 orange spots of the female *menapia* are represented by 2 marginal groups of vermilion scales, one in each section of the area. Vermilion scales occur nowhere else on the specimen, although those described above can be distinctly seen through the translucent scales of the upper surface.

THE FEMALE OF NEOPHASIA TERLOOTI.—*Under surface of hind wing.*—The vermilion markings are developed almost precisely in the positions of the orange markings of the female *menapia*—more strongly at the margin and the extreme base of the wing, but much less so elsewhere. The lower section of area 1c is, however, richly marked with vermilion for $\frac{1}{2}$ of its length from the base. The rest of the colored markings are light yellow of an ochreish tint, rather distinctly different from that seen elsewhere on the wings.

Under surface of fore wing.—The marginal markings and the marginal part of the chief orange patch are also light yellow, but of a lemon tinge. The orange of the chief marking and of scattered scales forming a linear mark in the cell is very rich and deep in tint: the mark in the cell is in fact better described as orange-red. The two marks at the end of the cell, in areas 5 and 6, are transitional in tint between the yellow marginal and the more central orange markings, and there is transition to be observed between the yellow margin in areas 1a and 1b and the rest of the chief orange marking. These changes in color are effected by a gradual increase in the number of orange scales and not by any real transition between the yellow and orange pigments, although if we study the wings as a whole we find several tints of orange and yellow.

Upper surface of hind wing.—The vermilion markings are represented by comparatively few scales. Within these markings the submarginal spots and the ground-color of the rest of the wing are deep orange, but of a duller tint than that of the fore wing. The submarginal spots of the outer (hind) margin are slightly less deep in tint, while along the costa, where the surface is concealed beneath the fore wing, the orange scales are gradually replaced by yellow, and again, at the extreme margin, by black, with perhaps a trace of the vermilion which is so distinct on the opposite surface. The vermilion scales could not be properly investigated because of the overlap of the wings.

Upper surface of the fore wing.—The colors are nearly as on the under surface, but, except at the apex, the submarginal spots and the margin of the principal marking are distinctly less pale and

therefore much nearer to the tint of the orange ground-color of the rest of the wing. The transition here does not appear to be effected by a gradually increasing number of deep orange scales, but by a gradual increase in the depth of the tint. The two marks at the end of the cell are nearly as rich an orange as in the expanse below the cell, and the transition towards yellow is, on the upper surface as compared with the lower, shifted towards the costal margin, occurring in the two spots of the same series placed *above* the end of the cell in areas 10 and 11. The linear spot in area 11 is yellow with thinly scattered orange scales, which are far more thickly placed on the spot in area 10.

7. THE COLORED PIGMENTS OF THE PIERINÆ AS ILLUSTRATED BY NEOPHASIA.

Professor F. Gowland Hopkins has shown (11, 12) that the white pigment of Pierines is an impure uric acid, and that the yellow orange and probably the red pigments are a derivative of uric acid which he calls "lepidotic acid." No pigments of similar constitution were found in any other butterflies. Therefore, when a Pierine mimics an Ithomiine or, as in *N. terlooiti*, a Danaine, the resemblance is effected by the production of an entirely different coloring matter. Gowland Hopkins believes that the yellow, orange, and red Pierine pigments are chemically nearly allied and may pass one into the other by slight changes perhaps in the degree of oxidation. He observed that one tint was represented by another in corresponding markings of opposite sexes or allied species. Thus he remarks (12, p. 678):

"It is interesting to note, by comparing various allied species of *Delias*, that the red marginal spot may become more yellow, while the yellow area usually found at the root of the wing may become more red, till both may exhibit a uniform orange colour, or the change may go farther and red and yellow change places without the general color-plan of the wing being altered."

These conclusions are strongly supported by a careful study of *Neophasia*, where it has been shown that in different individuals of the same sex of *menapia* the same markings may be either orange, orange-red, or pale vermilion, while in the opposite sex they may be absent or feebly represented in dull orange or yellow. Again in the allied *terlooiti* the corresponding markings are a rich deep vermilion in both sexes. We are led to realize that it is very easy for *Neophasia* to produce any shade between a pale lemon-yellow and a rich vermilion. The colored markings of *menapia* cannot be regarded as

mimetic, and, if *Danaida plexippus* had never entered America, it is highly improbable that anything more than the corresponding colored markings would have been evolved on the wings of the female *terlooti*. The range of tints in the markings common to *menapia* and *terlooti* gives an indication of the variational material out of which selection built up the mimetic pattern. The peculiar shade of yellow of the under surface of the hind wing, the rich orange of the central parts of the upper surface, the paler tints of the marginal markings, especially at the apex of the fore wing, the emphasis by black pigment of the veins of the hind wing upper surface, are all elements in producing the result—a somewhat rough but at a distance almost certainly a deceptive mimetic likeness to *D. plexippus*.

The same considerations help us to understand the prevalence of Pierine mimicry in tropical America as compared with other parts of the world—because of the predominant *Ithomiinæ* and *Danainæ* with warning patterns made up of reds, yellows, whites, and blacks. Such patterns are mimicked by the Pierine genera *Dismorphia* (in the broad sense), *Perrhybris* (“*Mylothris*”), *Archonias*, *Hesperocharis*, and we can now add the North American *Neophasia*.

8. THE RESTRICTION OF SEX-LIMITED INHERITANCE TO THE MIMETIC PATTERN OF NEOPHASIA TERLOOTI.

The older colored markings common to the females of *menapia* and *terlooti* are only partially sex-limited, being inherited in a very reduced form by some of the males of the former species and probably by all of the latter. The more modern mimetic pattern of the female *terlooti* is strictly sex-limited. The facts harmonize with the hypothesis that female mimicry is largely due to the great variability of this sex in Lepidoptera and the freedom with which it offers to selection a wide range of sex-limited colors and markings, but that when a pattern has been long established it tends to be transferred to the opposite sex.

The older non-mimetic marginal markings suggest that the transformation of uric into lepidotic acid is especially easy in this part of the hind wing and invite comparison with the number of mimetic Neotropical Pierines in which marginal or submarginal reds have been developed in the same position, viz., on the under surface of the hind wing—a study that would carry me too far from the subject of the present paper.

9. THE EVOLUTION OF LIMENITIS (BASILARCHIA) ARCHIPPUS FROM
AN ANCESTOR WITH A PATTERN LIKE THAT OF
L. (B.) ARTHEMIS.

The origin of *archippus*, suggested in the title of this section, is due to Scudder (6, 277-8, 714). All I have done is to support the published views of this distinguished naturalist by making a careful analysis of the markings of *archippus* and *arthemis*, by this means demonstrating that the details of the mimetic pattern are accounted for on his hypothesis. I am sorry to find that neither Scudder's hypothesis nor the results of my analysis carry any conviction to Dr. Skinner, who uses the following words: "*Arthemis* and *weidemeyeri* [with a very similar pattern] have flourished prosperously in the struggle for existence, and it is difficult to understand why *archippus* should be so specially favored. The statements attempting to prove the evolution of *archippus* from an ancestral form (*arthemis*) seem to me very inconclusive" (32, p. 127). Dr. Skinner makes no alternative suggestion as to the origin of the mimetic species. The doctrine of evolution—for it is hardly necessary to discuss the ancient belief which would assume that *archippus* was originally created in its present form—leaves us only two hypotheses. Either *archippus* was evolved from some form of *Limenitis* which has entirely disappeared or from one which is more or less closely represented by a species still in existence. The former alternative abandons the problem as insoluble, and abandoned it must be if there is no sufficient evidence that the ancestor can be reconstructed from any existing form. I agree with Scudder in preferring the counsel of hope to the counsel of despair. *L. (B.) arthemis* and *weidemeyeri* present us with an ancestral pattern wide-spread in the genus and found not only in North America, but also with little change in the Old World section of the temperate circumpolar zone. *Archippus* is so closely related to *arthemis* that the larval and pupal stages are almost identical, and although the imaginal patterns are so different, Scudder indicated, and I have attempted to trace in detail, the manner in which one pattern may be derived from the other. I really think that if Dr. Skinner, with specimens of *archippus* and *arthemis* before him, will verify the details of the account in my earlier paper (21, pp. 456-459), he will find that many minute features on the wings of the mimetic species are interpreted and correlated in a satisfactory manner. And a hypothesis that interprets stands, until replaced by another that interprets better.

With regard to Skinner's inference that inasmuch as *arthemis*

flourishes prosperously, it is unlikely that a mimetic form would arise from it, this is an objection which at once arises when mimicry is studied in the original monograph of its founder, published long before Fritz Müller had thought of his hypothesis. According to Bates, mimicry was a refuge for the destitute, a last means of escape for a hard-pressed and dying species. It was this very conclusion which was Müller's stumbling-block; for the majority of the mimics in southeast Brazil where he lived were clearly successful and abundant species, and the same is true of the majority of mimicking species wherever they are thoroughly known. Nor is there any reason to suppose that these successful forms originally arose from rare and hard-pressed non-mimetic ancestors. Want of space prevents the discussion of more than a single example. I refer to *Tirumala* (*Melinda*) *formosa*, an Oriental invader into the Ethiopian Region (18, 31). This species, abundant east of the Victoria Nyanza, near Nairobi, is there beautifully mimicked by the Ethiopian *Papilio rex*. The invading Danaine has transformed an indigenous species just as in North America. West of the great lake *T. formosa* is represented by an equally flourishing daughter species, *T. mercedonia*, with a pattern darker than its parent and one much further removed from the allied Oriental *Danainæ*. *Papilio rex* west of the lake becomes *P. mimeticus*, as beautiful a mimic of *T. mercedonia* as *rex* is of *formosa*. The two Danaine models are now distinct species, but their Papilionine mimics, connected by intermediates (*P. commixtus*) in the intermediate geographical area northeast of the Victoria Nyanza, are certainly a single interbreeding community. Similarly, in North America *Danaida plexippus* is a very distinct species from *D. berenice* and *D. strigosa*, although these latter may be geographical races of one species. The three forms of *Limenitis* are, on the other hand, all probably mimetic modifications of a single species, although *L. obsoleta* is probably distinct from *archippus* and *floridensis*. To continue the history of the African invading Danaines: Further westward the flourishing and prosperous *T. mercedonia* has given rise to a still darker species, *T. morgeni*, which has altogether lost the appearance of an Oriental *Tirumala* and has become the most perfect mimic of the African Danaine genus *Amauris*.

Here, then, we have a species so dominant that it is mimicked by a butterfly of a different family. It gives rise to another species and the mimic undergoes corresponding changes. Finally, in spite of these evidences of prosperity, it becomes itself a singularly perfect mimic. All these changes are far less abrupt than that from *arthemis*

to *archippus*, and I do not think that any naturalist who recognized the traces of the pattern of *mercedonia* still lingering almost invisible on the surface of *morgeni* or concealed by the overlap of the wings would doubt that the former is the ancestor of the latter and that the model has become itself a mimic.

Finally, it must be remembered that *L. archippus* has a far wider range than *arthemis*, and it is reasonable to suppose that this advantage has been conferred by its mimetic pattern. *Arthemis* is confined to Canada east of the Rockies and to the northeastern States, while *archippus* is "found over very nearly the same area as *Anosia plexippus*" (6, 278).

10. THE RELATION OF THE PATTERN OF LIMENITIS OBSOLETA (HULSTI) TO THAT OF ARCHIPPUS, ARTHEMIS AND WEIDEMEYERI.

When I wrote the paper criticised by Dr. Skinner (22), as well as an earlier paper, in some respects more detailed (21), I had never been given the opportunity of examining a series of the Arizona and Utah mimic, *Limenitis obsoleta (hulsti)*, and my brief account was founded on the excellent fig. 5 on plate VII of Dr. W. J. Holland's work (17.) In January, 1909, when I had the honor of representing my country at the Darwin centenary in America, my friend Dr. F. A. Lucas, Director of the American Museum, Central Park, New York, showed me a series of *obsoleta* together with its model, *Danaida strigosa*. The specimens were in the Brooklyn Museum, of which Dr. Lucas was then Curator. I saw at once that the form was very variable and that my work required the study and comparison of a long series of individuals. Dr. Lucas very kindly obtained a few specimens of the model and mimic for me and put me in communication with Dr. R. E. Kunzé, of Phoenix, Arizona, who has generously provided me with a fine mass of material. The following account has been drawn up from the study of 24 males and 9 females from Phoenix and 2 males and 1 female from Tucson. Thirty-three specimens bear the precise date of capture, one the month and year, one a month of which the interpretation is uncertain, and one for which the month is not recorded. Omitting these last two, the dates of capture are given in the following table. The three 1896 specimens were captured at Tucson (2,400 feet) in southern Arizona, the remaining 31 at Phoenix (1,100 feet) in the valley of the Salt River, southern Arizona.

| | | | |
|--------------------|-----|--------------------|-----|
| Apr. 9, 1896..... | 1 ♀ | June 6, 1896..... | 1 ♂ |
| Apr. 10, 1896..... | 1 ♂ | Apr. 22, 1897..... | 1 ♂ |

| | | | |
|----------------------|---------|---------------------|------------------|
| Apr. 17, 1909..... | 1 ♀ | July 30, 1910..... | 1 ♂ |
| Sept. 21, 1909..... | 1 ♂ | Oct. 5, 1910..... | 4 ♂ ² |
| Sept. 30, 1909..... | 1 ♀ | Oct. 7, 1910..... | 3 ♂ 1 ♀ |
| Oct. 27, 1909..... | 1 ♂ | Apr. 11, 1911..... | 1 ♀ |
| Oct., 1909..... | 1 ♂ | Apr. 15, 1911..... | 1 ♂ |
| Mar. 26, 1910..... | 1 ♂ 1 ♀ | Apr. 22, 1911..... | 2 ♂ |
| Mar. 27, 1910..... | 1 ♂ | Sept. 5, 1911..... | 1 ♀ |
| Mar. 29, 1910..... | 1 ♀ | Sept. 11, 1911..... | 1 ♀ |
| Apr. 1, 1910..... | 1 ♂ | Sept. 21, 1911..... | 1 ♂ |
| Apr. 4, 1910..... | 1 ♂ | Sept. 24, 1911..... | 1 ♂ |
| Apr. 6, 1910..... | 1 ♂ | Oct. 4, 1911..... | 1 ♂ |

The existence of two broods, one emerging between the end of March and the end of April, the other in September and October, are clearly shown. The two specimens in June and July, respectively, were probably representatives of a third brood.

The model, *Danaida strigosa*, appears to be much rarer than its mimic at Phoenix—at any rate, in the localities where Dr. Kunzé collected. From this place I have only received 2 males, captured July 2 and 6, 1912; from Tucson—1 female May 26, 1 male June 7, 1 female June 9, 1 male August 19, all in 1896; from Prescott (5,400 feet), in western Arizona—2 males and 1 female July 15, 1912.

Dr. R. E. Kunzé, of Phoenix, Arizona, who has had a long and intimate experience of the butterfly fauna of the State, kindly informs me that, in the Phoenix (1,100 feet) and Tucson (2,400 feet) districts and between them, *L. obsoleta* is almost exclusively found in the valleys, along the river-bottoms, and by the canals, where its larval food-plant, a willow, grows.³ It is commoner in the river-bottoms, especially near the streams, than by the canals. *Danaida strigosa* flies with it in these situations and is indeed commoner there than elsewhere, but, unlike the mimic, it is also found in other places. It is impossible to state the relative proportions of Danaine and *Limenitis*, but by the rivers and canals the mimic is the commoner in the ratio of about twelve or fifteen to one. The proportions at Tucson and Phoenix seem to be the same.

Danaida plexippus occurs, but is scarce in the Salt River valley at Phoenix. Dr. Kunzé estimates that it may exist in the ratio of one to fifteen of *D. strigosa*, but in some seasons he does not meet with

² The armatures of two of these males were studied by Dr. Eltringham (p. 190).

³ Dr. Kunzé adds in his letter of August 5, 1913: "I should say that *obsoleta* has here [Phoenix] from 3-4 broods in a season, from April 1st up to November 1st, in a mild autumn, of course. I think the last brood oviposits on cottonwood, our *Populus fremonti* and other species, because its leaves keep green till latter part of December, whereas willow drops leaves earlier."

it at all. At Prescott, Arizona (5,350 feet), 135 miles north of Phoenix, *strigosa* flies in the company of *plexippus* from July to September, the latter being the commoner of the two. *D. strigosa* extends as far south as Galveston, Texas, and may also occur in some parts of Mexico, near the northern boundary. *Limenitis obsoleta* does not occur at Prescott.

The fine series of *L. obsoleta* (*hulsti*) tabulated on p. 180 at once made clear to me that the Arizona form is not, like *floridensis* (*eros*) in Florida, a local race of *L. archippus* transformed by mimicry of the dominant local *Danaine*, but the bearer of an ancestral pattern which preserves features lost by the two other mimetic races. I therefore desire to correct my former conclusion, founded on the figure of a single specimen, that *obsoleta* is a modified form of *archippus* (21, p. 460, 22, pp. 171-2). At the same time I remarked in the latter paper (p. 172): "I have not yet had the opportunity of ascertaining whether this hypothesis is supported by evidence derived from a careful study of the pattern."

The hind wing.—The most prominent ancestral features of *obsoleta* are the traces of the white discal band derived from an ancestor with a pattern like that of *arthemis* or *weidemeyeri*. In *archippus* and *floridensis* a trace of the white band is found on the under side of the hind wing in some specimens, but so far as my experience goes never on the upper surface. In *obsoleta* some trace of it is always present on both surfaces, but when, as in the majority of specimens, there is a difference in the degree of development, it is stronger upon the under side. It is more strongly developed in the females than the males, and this is the general rule with the ancestral features of the species, as it appears to be in *archippus*, of which a certain proportion of the males in the Albany district, but no females, have entirely lost the black discal stripe from the upper surface of the hind wing (recorded by Mr. John H. Cook, 22, pp. 211-212). Thus the white stripe, together with its black outer border, is evanescent on the upper surface of the hind wing of 2 female *obsoleta* from Phoenix and small in the female from Tucson, whereas the same feature is evanescent in half the males from Phoenix and but slightly developed in others. The evanescent feature in both males and females is more strongly represented, generally far more strongly, on the under surface. The degree of development of the black band is generally related to that of the white, the two being usually evanescent together or well developed together, but the range of variation is much greater in the white than in the black, corresponding with the entire disappearance

of the former but not of the latter from the upper surface of the allied *archippus*. On the other hand, the development on the under as compared with the upper surface is greater in the black than the white. In both sexes there is a tendency, as in *archippus*, to throw the white spots on the under surface of the hind wing into relief by an inner edging—a darkened shade of the ground-color in areas 2, 3, 4, and 5, still darker and often black in areas 6 and 7. This feature probably represents the black inner border of the white discal band in the non-mimetic ancestor.

When the 32 specimens, omitting the 2 taken in June and July, recorded in the table on p. 180, are arranged according to their two broods—the 15 March and April specimens together and the 17 September and October together—it is seen that there is a small but distinct seasonal difference in the development of the trace of the white discal band of the hind wing and its black outer border. The spring brood is in this respect distinctly the more ancestral, bearing on the average stronger traces of the pattern of *weidemeyeri* and *arthemis*. This is true of the females as well as the males, as may be inferred from the following statement:

Females (spring brood = 4, autumn brood = 5).—The only 2 specimens with evanescent band and border bear the dates Sept. 11, 1911, and Oct. 10, 1910. The most reduced band of the spring brood is seen in the Tucson specimen, April 9, 1896. In all the remaining 4 spring females, the band and, in all but one, the border is distinctly stronger than in either of the 2 remaining autumn females.

Males (spring brood = 10, autumn brood = 13).—It is extremely difficult to classify the degree of development of the band and border—there is a complete and gradual transition. There is, however, a marked difference at both ends of the scale between the two broods. The most evanescent white bands are seen in 6 autumn males. In all these the feature is more reduced than in any spring male. Very small and reduced bands are found in 3 males of each brood. Beyond these there is the most gradual transition to the highest degree of development found in the sex, and among these we find by far the highest in a specimen captured April 22, 1911, while 2 other spring males are rather beyond any of the autumn brood. Considering the black border separately, the difference is even more marked, for this feature is evanescent in 4 of the autumn brood and none of the spring, while the next 4 are equalled and on the whole slightly exceeded by the 4 spring specimens in which the feature is least developed. The black border is more highly developed in 4 of the spring

brood than in any of the autumn. This detailed comparison has been extraordinarily difficult to make, because of the perfect transition and the minute shades of difference. When the attempt was made to express the difference, the specimens grouped themselves into fours in an irritating and unnatural manner. It might perhaps have been wiser to attempt no analysis of so transitional a feature, but to be contented with the statement that a distinct difference exists at both ends of the scale, the band and border of the most strongly marked specimens being decidedly more developed in the spring brood, while the reduction of these features in the least strongly marked specimens was carried distinctly further in the autumn brood. I cannot but think, however, that my attempts at an analytical comparison, whatever faults there may be in the details, are a truer expression of the facts.

An interesting difference between the upper surface of *obsoleta* and that of *archippus* is common to both fore and hind wings, viz., the far more heavily blackened veins gained by the latter in mimicry of *D. plexippus*. *Floridensis* here shows its origin from *archippus*, for it retains the darkening along the veins, although out of place in a mimic of *D. berenice*. No such evidence of having passed through an *archippus* stage is to be seen on the upper surface of *obsoleta*. The veins are heavily blackened on the under surface of the hind wing in all three mimics, in evident likeness to their respective models, although *obsoleta* in this respect is less darkened and a less perfect mimic than the other two.

In certain specimens of *obsoleta* there is to be seen on the hind wing under surface two largish rich brown sharply outlined patches, one in the cell and one near the base of area 7. On the basal side of each patch is a white spot and a white suffusion commonly surrounds the projection of the precostal into area 8. These elements tend to become evanescent together and distinct together, acting like a single feature. Slight traces of these markings can probably be found on every fresh specimen. They were remarkably pronounced in the female taken Sept. 5, 1911 (p. 181). These vestiges, except in one respect, resemble the well-known basal pattern of *arthemis* far more closely than that of *weidemeyeri*. The pale elements are, however, for the most part blue in *arthemis*, but nearly white in *weidemeyeri*, and therefore in this respect nearer to *obsoleta*. *Archippus* has advanced further from the ancestral forms than *obsoleta*, for "the basal red patches have vanished, but the pale blue marks in and on the costal side [area 7] of the base of the cell are retained, and,

lightened in tint, represent the two more conspicuous white spots occupying nearly the same position in *Anosia* [*Danaida*]" (21, 456-7). Now that I have had the advantage of studying *obsoleta*, and have re-examined *archippus* in the light of the new experience, I find that a few examples do possess a very faint trace of the reddish patches of *arthemis*. In these vestiges as in so many other features in the pattern we are led to conclude that *obsoleta* represents an older stage in the evolution of *archippus*.

The fore wing.—The inner edge of the angulated black outer border of the white band of *arthemis* and *weidemeyeri* runs from the costa to the inner margin of the wing, near but well within the posterior angle, although it is broadened so far that its outer edge enters this angle; in most specimens of *archippus* it runs to the junction of the middle and posterior third of the outer (hind) margin (21, p. 457). Some females, however, approach the condition of *obsoleta*, which is generally far nearer in this respect to the pattern of *arthemis* and *weidemeyeri*. In *obsoleta* the direction of the vestigial black outer border, which, except near the costa, is evanescent on the upper surface, can be easily traced by fixing the attention on the outer ends of the four prominent white spots in areas 3, 4, 5, and 6. With this as guide, the eye is led on to an evanescent white spot nearly always present in area 2, and in certain individuals to the faint continuation of the black line towards the posterior angle. The angle made with the costa is very different from that of *archippus*. The black line is usually far more distinct on the under surface, and here it may be seen in many specimens that the direction changes abruptly in area 1b, becoming parallel with the outer margin and leading to a termination on the inner margin within, and often well within the posterior angle. In well-marked specimens, especially in the females, the black line is seen to lead to the outer end of a white linear mark close to the inner margin in area 1a (see p. 186). Faint vestiges of the former white band can even be made out in 1b on the under surface of a few individuals. There is great variation in the position of the black line in 1b. In most males it unites with and continues as a broadening of the black margin.

The white spots which represent the costal half of the white band of *arthemis* and *weidemeyeri* are far better developed in *obsoleta* than in *archippus*. In the latter the spots are 2 to 4 in number, the last being very small. In *obsoleta* there are always 4 large and distinct spots, especially well developed in the female, while a minute 5th spot, already mentioned as placed in area 2, is nearly always present

and often more strongly marked on the under surface. A trace of it could be made out on the upper surface of all the females and on 17 of the males; from one or both sides of the remaining males it was absent, but it is likely that when these were fresh examination with a lens would have led to the detection of a few white scales. It is clear that the trace of the original discal band is more shortened in *archippus* than in the Arizona form, and that the 4th spot in area 3, or in other individuals the 3rd in area 4, is now in the position of the minute trace of a 5th spot in area 2 of *obsoleta*. Furthermore, the black discal marking retains in *obsoleta* more of its original appearance as an outer edging to the white band than in *archippus*—an appearance still more fully sustained upon the hind wing. In the fore wing of *archippus* it is obviously much developed, especially at the costal end, in mimicry of the model *plexippus*.

The trace, on the costa itself, of the anterior end of the white band of the fore wing, already described as generally to be found in *archippus* (21, p. 457), was present in all the females and 19 males of *obsoleta*, but in some of these it was barely visible. This feature is apparently more often wanting altogether from *archippus*, but the two forms have reached nearly the same level, and I think that in both examination with a lens would reveal the presence of some trace of the marking in most or perhaps all fresh specimens.

I have already incidentally mentioned on p. 185 the most interesting ancestral feature in the fore-wing pattern of *obsoleta*, and one entirely wanting from *archippus*, viz., a distinct trace in area 1a of the inner marginal end of a white discal band like that of *arthemis* or *weidemeyeri*. This linear mark was present, varying in the degree of its development, in all the females and 23 males, and traces might probably have been found on all when fresh. The mark is also to be found on the under surface where the fore wing is overlapped by the hind, but for this reason it was only examined in a few specimens; in these it did not stand out on the paler ground-color as conspicuously as on the upper surface. It has been already pointed out on p. 185 that the outer end of the mark coincides with the point on the inner margin indicated by the direction of the vestige of the black outer border in some individuals, viz., a point well within the posterior angle of the fore wing. In a single female (Apr. 17, 1909), unfortunately rather worn, the mark in 1a apparently extends to the black margin at the posterior angle. The same relationship to a mark stopping short of the angle is also indicated, especially in fresh specimens of the female, by a distinctly

paler shade of the ground-color outside the discal black stripe on both surfaces of both wings. The change of shade follows the suggested direction of the black line to the inner margin of the fore wing, although near this border it is not sharply demarcated as on the rest of the wing. Such an abrupt change in the depth of the color is very rarely to be seen on the upper surface of *archippus*. Scudder has looked on the reddish spots of *arthemis*, occupying the very position of this paler shade in *obsoleta*, as the foundation from which the mimetic form arose (6, p. 714), and I have followed him (21, 22). If we are right, and the transformation occurred first in this area and only later in the area inside the white discal stripe, it is easy to understand why there should be a difference in the shade of the ground-color for natural selection to seize upon. The Arizona *Danaida strigosa* is also paler on the outer than it is on the inner part of the wings, although the transition is gradual and not sharp as in *obsoleta*. On the under surface of the fore wing *archippus* is, in this very respect, more strikingly ancestral than *obsoleta*, the pattern of the model having been such as to emphasize the feature. *Archippus* is also commonly ancestral as compared with *obsoleta* in the distinct indication by a reddish-brown tint of the red submarginal spots on the under surface of both wings (21, p. 456).

The white mark in area 1a of the fore wing has this further interest, that it indicates the point at which the outer edge of the discal band of the hind wing met that of the fore, reconstructing for us a pattern like that of *weidemeyeri* and *arthemis* in which the band of the hind wing is placed much further from the outer margin than it is in the other wing. The evolution of the marginal pattern of both surfaces of both wings of *obsoleta* from a condition like that of *arthemis* appears to have been the same as in *archippus* (21, pp. 456-459) and to have reached nearly the same result. The slight differences correspond with those between the respective models and are doubtless due to mimicry.

The two white spots in the fore wing cell on the under side were present in all the males of *obsoleta*. The females showed greater variability, the basal spot being sometimes absent, but generally much larger than in the males. On the upper surface of the same wing the distal spot was large, for this feature, in 6 females, small in 3, minute in 1. In 14 males it was sharp and distinct, though small, and it could be detected in 8 of the others. In the remainder the triangular black mark in which the white spot lies could be made out by looking carefully for it. White scales were probably origin-

ally present on this mark in some of the worn specimens that do not now possess them. This white spot can be far more frequently detected on the upper surface of *obsoleta* and *archippus* than on that of *arthemis* and probably more often than in *weidermeyer*i, although it may attain great relative size in this species (21, Pl. XXV, fig. 1). Its frequent appearance in the two mimics points to an origin from an ancestor of the existing North American species that was in this respect nearer in pattern to *L. lorquini*, in which the spot is almost invariably well developed (21, 479, 480, Pl. XXV, figs. 6-8). At the same time the redevelopment of an ancestral feature by means of mimicry must not be lost sight of as a probable interpretation. The pattern of *D. strigosa* is such that the spot in the fore-wing cell of *obsoleta* probably adds to the likeness, at any rate during flight. The strong development of the feature in the females—in this species the more ancestral sex—favors the former hypothesis. As regards the traces of the *Limenitis* pattern persisting in the fore-wing cell on the under surface and their transference to the upper surface, *obsoleta* and *archippus* have reached nearly the same stage. The most strongly marked individuals of the former are, however, more ancestral, in that the white spot on the upper surface and the two spots below are larger and more conspicuous than in any examples of *archippus*.

The seasonal differences on the fore wing were not so well marked as on the hind. Furthermore, the relationship was reversed, the autumn brood being more ancestral than the spring. The difference, however, was barely detectable except in one feature where it was very distinct—the minute white spot in the fore-wing cell. This was sharp and distinct in 11 out of 13 autumn males and only 2 out of 10 spring males. It was also on the whole better developed in the autumn females.

Temperature experiments on the pupæ and, if possible, on the ova and larvæ would be well worth trying on this form as well as on *archippus* and *floridensis*. Considering what has been done by Dorfmeister, Weismann, Merrifield, and Standfuss, remembering also that Lamborn has recently brought evidence which suggests, although it does not prove, that vestiges of "tails" can be brought back to the hind wings of the tailless mimetic females of *Papilio dardanus* (26), it is quite probable that some increase in the pattern derived from a non-mimetic ancestor might be induced by the shock of heat or cold applied to the pupal or both larval and pupal stages. And the fact that there are certainly some seasonal differences in the

ancestral elements of *L. obsoleta* renders such experiments especially hopeful.

An experiment made by Edwards and quoted by Scudder (6, p. 278) is also encouraging. The black band of the hind wing of *archippus* was widened in two butterflies which emerged from pupæ subjected to cold, being in one specimen, a female, nearly three times the normal width.

It is necessary, in conclusion, to point out in a few words some special effects of the Danaine model, *D. strigosa*. Most prominent among these is the peculiar shade of the ground-color of *obsoleta*, so different from that of *archippus* and *floridensis* and so strikingly like that of the model. The triangular shape of the discal spots of the fore wing, especially pronounced in those of areas 3 and 4, has evidently been produced in mimicry of the characteristic-looking triangular and diamond-shaped spots of the model. The direction of the line of these spots in *obsoleta* which has been shown on p. 185 to be more ancestral, viz., more like that of *arthemis* and *weidemeyeri*, than in *archippus*, has doubtless been stereotyped by the model, in which four of the most conspicuous white spots in areas 1b, 2, 3, and 4 are parallel with the outer margin of the fore wing. It is also probable, as suggested in a former paper (21, p. 460), that the retention of the white spots representing the discal band on the hind wing upper surface, and it may be added the linear mark in area 1a of the fore wing, has been aided by "a general likeness" [during flight] "to the pale-streaked hind-wings of *strigosa*." Here, too, the relative development of the feature in the female favors a different interpretation; for, as already pointed out (p. 182), the female is slightly the more ancestral and the male the more advanced mimic in this species. The fact that the traces of the black border of the white discal band, which undoubtedly interfere with the mimetic resemblance, on the whole follow the white spots in the degree of development (p. 182) is also in favor of the supposition that the entire marking is an ancestral feature which has not yet been got rid of.

In order to prove that *obsoleta* is, as its pattern strongly suggests, ancestral as compared with *archippus*—that it stands in a position intermediate between the latter form and the non-mimetic species of *Limenitis*—*arthemis* and *weidemeyeri*—it is necessary to seek for another line of evidence.

11. THE MALE GENITAL ARMATURE OF THE NORTH AMERICAN FORMS OF LIMENITIS.

In former years I have felt, with many other naturalists, some suspicion of the conclusions based on a study of the male genitalia of Lepidoptera. The organs are so complex and in parts so thin-walled, so liable to be deformed by twisting and pressure, that it seemed unlikely that they could escape alteration in the processes of manipulation and mounting. Their shapes are such that a slight difference in the angle at which a drawing is made or a photograph taken makes all the difference to the result. I have, however, been converted by my experience of the work of my friends Dr. Karl Jordan and Dr. H. Eltringham. I have seen the latter naturalist preparing and studying the same parts in different individuals again and again until he was able to determine with complete certainty the actual form that is characteristic of the species or race. I therefore asked him if he would kindly help me by preparing and drawing the genitalia of the North American forms of *Limenitis*. In asking this favor, I was, all unconsciously, making ready for a most valuable test of the validity of the method and its results. At the time when Eltringham made his drawings we had no copy of Scudder's great work (6) available, but, when they were finished, I borrowed the volumes from the library of the Entomological Society of London. I turned at once to Plate 33, representing the genitalia of the Canadian and eastern North American species of *Limenitis*, and found that the four figures (9, 11, 12, 15), prepared by Edward Burgess for Scudder, might almost have been copied from Eltringham's drawings or the drawings from the figures! Two careful pieces of work carried out independently have led to precisely the same result. It will therefore be admitted that we may safely accept the six figures on the accompanying Plate V as the expression of the true structural relationships in the different species.

Figures 4, 5, and 6 on the right side of Plate V represent the male genital armatures of species also figured by Scudder, save that his *L. astyanax* (fig. 15) represents the eastern race and Eltringham's (fig. 4) that from Arizona. But the form of the genitalia is nearly the same, as may be seen by comparing the figures, allowing of course for the difference in magnification. Eltringham's figures also show with Scudder's the close resemblance between *astyanax* and *arthemis* (fig. 5, Scudder's fig. 9). The two representations of *L. archippus* are almost identical, save that Scudder (figs. 11 and

12) represents the end of the terminal hook as obliquely truncated, Eltringham (fig. 6) as a simple point.

Figures 1, 2, and 3 on the left of the plate represent forms of *Limenitis* from an area outside the limits of Scudder's monograph. The claspers of *L. lorquini* (fig. 1) are seen to differ markedly from those of all the other forms. *Weidemeyeri* (fig. 2), on the other hand, closely resembles *arthemis* and *astyanax*, although it is of a stouter build. The main interest of the series of figures is, however, concentrated in *obsoleta* (fig. 3). Just as the pattern of this species was seen to be intermediate in many details between that of *archippus* on the one hand and *arthemis* and *weidemeyeri* on the other, so is it with the form of its claspers. To make sure that the appearance represented in fig. 3 was not an individual peculiarity, Dr. Eltringham made a second preparation, but with precisely the same results. The comparison between figs. 2 and 3 suggests that the mimetic form arose from an ancestral species with claspers more like those of *weidemeyeri* than *arthemis*. Looking at these figures, some naturalists may be inclined to suppose that *obsoleta* sprang from *weidemeyeri* in the southwest, while *archippus* developed independently from *arthemis* in the east and north. Such a conclusion seems to me improbable. It is unlikely that independent lines of evolution would have led to structures with the essential similarity that is to be recognized between the forms shown in figs. 3 and 6—I refer especially to the hook below and the strong teeth above the end of the organ—and still more improbable that such independent evolution would have led to the resemblances in minute detail that have been shown to exist between the patterns of *obsoleta* and *archippus*.

Remembering that these conclusions are founded on small differences between organs that are themselves very variable, Dr. Eltringham has confirmed his results by making preparations from 3 individuals of *archippus*, 2 of *obsoleta*, 2 of *weidemeyeri*, and 2 of *astyanax arizonensis*. He finds that the fine points or teeth are not only variable in different individuals, but that they vary on the two sides of the same individual. This he has shown by the careful drawings reproduced on Plate V, where this want of symmetry is apparent in nearly all the figures. The second specimen of *weidemeyeri* has rather fewer teeth than the one figured. In a single specimen of *archippus floridensis (eros)* the organs were somewhat larger than in *archippus* and the clasper points were a little less acute. In spite of great individual variability and the want of symmetry, the claspers of the individuals shown in Plate V exhibit recognizable characters

common to other individuals of each species examined by Eltringham and, as regards three of them, by Burgess.

Knowing my own want of experience in the comparative study of these male abdominal appendages, I submitted Dr. Eltringham's drawings to my friend Dr. Jordan, who wrote, Aug. 15, 1913: "*Archipus* appears to be a later modification of *obsoleta*, as you say. *Astyanax arizonensis*, *weidemeyeri*, and *arthemis* are also closely related to one another."⁴ Dr. Eltringham also agrees that the comparative study of the armatures supports the conclusions arrived at from a study of the patterns.

Considering together pattern and the structure of the claspers, there are strong reasons for believing that the mimetic forms arose from a North American *Limenitis* with the pattern of *arthemis* and *weidemeyeri*, but including a white spot in the fore-wing cell upper side now seen most commonly in *lorquini* among North American species, and with claspers like those of *weidemeyeri* and *arthemis*, but probably nearer to the former.

I trust that Dr. Skinner will consider that this evolutionary history, if not convincing before, has been rendered so by the fresh evidence now produced.

12. SIMILAR ENVIRONMENTAL CONDITIONS VERSUS MIMICRY AS AN INTERPRETATION OF COLOR RESEMBLANCES.

With regard to the resemblance of *Limenitis* (*Basilarchia*) *floridensis* to *Danaida berenice* in Florida and of *L. (B.) obsoleta (hulsti)* to *D. strigosa* in Arizona, Skinner suggests (32, p. 127) that "similar environmental conditions explain these color resemblances better

⁴ The remainder of Dr. Karl Jordan's letter contained an interesting and suggestive criticism of Scudder's conclusion that *proserpina* is a hybrid between *arthemis* and *astyanax*.

"The differences in the genitalia between *astyanax* and *arthemis* might render copulation a little difficult, but are too insignificant to prevent it. According to Scudder, *proserpina* is the hybrid between *astyanax* and *arthemis*. If that is the case, the genitalia should be intermediate. As they are identical (teste Scudder) with those of the northern insect, I do not believe that *proserpina* is a hybrid. The offspring of a ♀ *proserpina* were partly *proserpina*, partly *arthemis*. This also points in the direction that *astyanax* has no part in the production of *proserpina*. Scudder appears to rely particularly on this point—*proserpina* inclines towards *astyanax* where the latter prevails, and towards *arthemis* in the places where this insect is abundant. But such an agreement in coloration may simply be due to the two occurring side by side. It is not necessarily evidence for hybridization. I have only looked at Scudder's book, not at the specimens; my opinion is therefore worth very little, but I incline to the belief that *arthemis* assumes the pattern of *astyanax* where it comes into contact with the latter, i.e., that *proserpina* is a southern modification of *arthemis*, not a hybrid. It would be advisable, however, to examine the genitalia of a series of specimens of all three insects."

than the hypothesis of mimicry." He does not venture to suggest this interpretation for the resemblance of *L. (B.) archippus* to *Danaida plexippus*; for the great environmental changes endured by both model and mimic in their extensive north and south range make any such suggestion untenable. With regard to the detailed likeness of three forms of *Limenitis* to three Danaine butterflies in North America, I may fairly retaliate on my friend and point out in his own words, *mutatis mutandis*, that "it seems logical to consider that they are governed by a general law rather than that two of them, but not the third, are caused by similar environmental conditions." I have already many years ago dealt with this supposed interpretation of mimetic resemblance by an appeal to the forces of the environment, and the arguments then brought forward (15) have, so far as I am aware, never been met. Dr. Skinner does not attempt to meet them, nor does he even allude to the peculiarly strong evidence furnished by these very North American mimics against the hypothesis of environmental conditions. Although this evidence is clearly set forth in the paper which Dr. Skinner was discussing (22), as well as in earlier publications of mine (16, 21), I will repeat the substance of it on the present occasion.

The three Danaines of North America are modern invaders from the Old World, quite isolated and out of place in the New, while the genus *Limenitis* is an ancestral element in the North American fauna. My own experience of insect systematics is very limited, and I could not with any confidence or authority attempt to weigh the value of characters which have been described as generic. Knowing these limitations only too well, I applied to my friend Dr. K. Jordan, and he, after making fresh investigations into the male genitalia and carefully studying Moore's generic characters, came to the conclusion that the Old World *Limnas* and *Salatura* and the New World *Anosia* and *Tasitia* could not be sustained as separate genera, but that all four were to be properly included in the single genus *Danaida*. This genus is nearly related to several much-mimicked groups of *Danainæ* in the Old World, but the two species from which the few American geographical forms have been derived are aliens in the New World.

Dr. G. B. Longstaff has recently shown that in the gregarious instinct, as manifested by hanging in festoons and clusters from trees, the Old World *Danaida genutia* (*plexippus*) resembles its New World representative *D. plexippus* (27, pp. 75, 76), in which the same habit has often been observed (6, pp. 730, 734-7)

Even in pattern there is but little difference between the most nearly allied Asiatic and American species of *Danaida*, and if, as Dr. Skinner believes, color and pattern are the expression of environmental conditions, then they are the expression of an Old World, and not of a New World environment. On Dr. Skinner's view, the Old World invader, when it became exposed to the new environment, should have come to resemble the New World resident. Instead of this, the resident has come to resemble the invader.

In concluding the present paper I may quote an opinion expressed to me by Professor Svante Arrhenius. A few years ago I asked my friend whether he thought it possible to explain by the incidence of physico-chemical forces, such as those of the environment, the superficial resemblance of one form to another when that resemblance required, as in the development of a complex pattern, the co-operation of many different factors. He replied, as I expected, that he did not consider the explanation possible; for the building up of such a likeness was inconceivable except by the aid of selection. This was the argument I advanced in 1898 (15), after an analysis which showed that mimetic resemblance often requires the co-operation of many different factors; and it was a great satisfaction to find the conclusion confirmed by an authority with Professor Arrhenius' broad outlook on the sciences in their relation to one another and to mathematics.

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EXPLANATION OF PLATE V.

Genital armatures of male North American *Limenitis* (*Basilarchia*). Figures drawn by H. Eltringham. All the figures are magnified about fourteen diameters.

- Fig. 1.—*Limenitis lorquini*.
 Fig. 2.—*L. weidemeyeri*.
 Fig. 3.—*L. obsoleta*.
 Fig. 4.—*L. astyanax arizonensis*.
 Fig. 5.—*L. arthemis*.
 Fig. 6.—*L. archippus*.



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