



MIMICRY AND THE INHERITANCE OF SMALL VARIATIONS

By Professor E. B. Poulton, F.R.S.

THE inheritance of small variations is an issue of such supreme importance that it would perhaps be well to devote the whole of the present article to its consideration. I will, at any rate, put it in the forefront, beginning by the quotation of two passages in which Darwin summed up the labour and the thought of half a lifetime.

“Any variation which is not inherited is unimportant for us. But the number and diversity of inheritable deviations of structure, both those of slight and those of considerable physiological importance, is endless. . . . No breeder doubts how strong is the tendency to inheritance: like produces like is his fundamental belief: doubts have been thrown on this principle by theoretical writers alone. . . . If strange and rare deviations of structure are truly inherited, less strange and commoner deviations may be freely admitted to be inheritable. Perhaps the correct way of viewing the whole subject, would be, to look at the inheritance of every character whatever as the rule, and non-inheritance as the anomaly.”*

“When a new character arises, whatever its nature may be, it generally tends to be inherited, at least in a temporary and sometimes in a most persistent manner. What can be more wonderful than that some trifling peculiarity, not primordially attached to the species, should be transmitted. . . .

“Some writers, who have not attended to natural history, have attempted to show that the force of inheritance has been much exaggerated. The breeders of animals would smile at such simplicity, . . .”†

Why should Professor Bateson, Professor Punnett and their followers make assertions which imply that Darwin was a hasty generaliser, that his opinions on fundamental questions were

* *Origin of Species*, 1st. ed., 1859, pp. 12, 13.

† *Variation of Animals and Plants under Domestication*, Vol. I., 1875, p. 446. The same conclusion is re-stated and examples given on pp. 447 and 449.

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ill-considered and of no importance? The answer is a simple one. These clever and ingenious men, dazzled and confused by a re-discovery of the utmost interest, and the exciting investigations to which it has led, have entirely lost all perspective and all sense of proportion. Their distorted vision is most unfortunate for English biological science, because young and vigorous naturalists, ever eager in the pursuit of some new thing, are being led into the same hopeless confusion which has overwhelmed their leaders. It is well that the danger should be seen and guarded against, that men should know how far these writers are to be taken seriously when they wander, as they are so apt to do, beyond the details of their own researches. The irresponsibility of de Vries's principal exponent in this country is manifest in the following passages quoted from the same volume* and only eleven pages apart:—

De Vries according to Bateson.

“First we must, as de Vries has shown, distinguish real, genetic variation from *fluctuational* variations, due to environmental and other accidents, which cannot be transmitted” (p. 95).

De Vries according to De Vries.

“Thus we see that the theory of the origin of species by means of natural selection is quite independent of the question, how the variations to be selected arise. They may arise slowly, from simple variations, or suddenly, by mutations; in both cases natural selection will take hold of them, will multiply them if they are beneficial, and in the course of time accumulate them, so as to produce that great diversity of organic life, which we so highly admire” (pp. 83, 84).

An even sharper contrast is evident between the following passages from the same authors. First, Professor Bateson:—

“For the first time he [de Vries] pointed out the clear distinction between the impermanent and non-transmissible variations which he speaks of as *fluctuations*, and the permanent and transmissible variations which he calls *mutations*.”†

Now Professor de Vries himself:—

“Sugar beets afford the finest example of the process of artificial

* *Darwin and Modern Science*, Cambridge, 1909.

† Mendel's *Principles of Heredity*, Cambridge, 1909, p. 287.

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selection. In no other plant under cultivation has the technique of selection reached so high a pitch of perfection; in no other is the method so sure or the result so certain. There is now no sale for beet seed which has not been the result of careful selection.

“Experiments in the selection of sugar capacity began about 1850. This instance shows best, therefore, what can be achieved within half a century by continued selection in one and the same direction, hand in hand with continual improvement of method.

“Progress has been enormous: the average content of the common beet, which at first was a matter of 7—8 %, is now double that amount. Shape, size, and weight, the character of the leaves and especially the reduction in woody tissues have all been the object of selection, and have made the beet much more valuable from the industrial point of view.

“All this has been done by selection of the best individuals afforded by ordinary fluctuating variation. Neither spontaneous variations nor crossings have played any part in it. We are dealing here with the process in its simplest form.”*

It is surely the irony of fate that I, who, admiring de Vries as an investigator, think nothing of his contributions to the evolution theory, regarding them as in part already to be found in Darwin and Galton and, when original, puerile—that I should have to correct his professed supporters and exponents, and explain the meaning of a de Vriesian “fluctuation” as contrasted with his “mutation.” The difference is *not* that the first are non-transmissible and the second hereditary, but that fluctuations are liable to regression and more and more liable to it the further they have been advanced in any direction by means of selection. Mutations, on the other hand, are a leap to a new position of genetic stability. In all these conceptions de Vries is merely following Galton, who earlier expressed the same conclusions far more clearly and with a much better terminology. I must add that a perfectly correct account of de Vries’ conclusions has been given by A. A. W. Hubrecht, † C. B. Davenport, ‡ R. H. Lock§ and J. Arthur Thomson.¶

* *Die Mutationstheorie*, English Translation by Farmer and Darbishire, Vol. I., 1910, pp. 99, 100.

† *Popular Science Monthly*, July, 1904, p. 205; *Contemporary Review*, No. V., 1908.

‡ *Fifty Years of Darwinism*, New York, 1909, pp. 173—4.

§ *Variation, Heredity and Evolution*, 2nd ed., London, 1909, pp. 75, 135—6, 155.

¶ *Heredity*, London, 1908, pp. 78, 98. Quotations from all these writers,

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In spite of de Vries himself, in spite of all that the above-named writers have said, a “de Vriesian mutation,” which is the same thing as Galton’s better-named “transilient variation,” is rapidly being replaced by a “Batesonian mutation,” which is the same thing as Weismann’s better-named “blastogenic variation”—also called by various writers at various times *constitutional*, *congenital*, *centrifugal*, *genetic*, *inborn*, *innate* and *inherent*. It is a formidable list, and the only objections to adding mutation to it are that it is the least descriptive, the most recently applied, and, because of its history, by far the most confusing term of a list that is already quite long enough.

Mighty is the force of fashion, in science as in other departments of human activity. Even my friend the Master of Christ’s College, Cambridge, who very nearly a quarter of a century ago laboured with Dr. Schönland and with me to make known Weismann’s conclusions on heredity, even he now hands over to de Vries what de Vries himself has never claimed, viz., Weismann’s clear distinction between blastogenic and somatogenic characters.* So also Clifford Dobell, in a passage with a wording which goes far to suggest Weismann’s term blastogenic, prefers to perpetuate this cause of confusion, error, and injustice:—

“By *mutation* . . . I mean a permanent change—however small it may be—which takes place in a bacterium and is then transmitted to subsequent generations. The word does not imply anything concerning the magnitude of the change, its suddenness, or the manner of its acquisition. The term denotes a change in genetic constitution. All other changes which are impermanent—depending generally upon changes of the environment—and not hereditarily fixed, are called *modifications*.”†

The word mutation—originally introduced by Waagen, used in a different sense by de Vries, used in a third sense erroneously ascribed to de Vries by Bateson—is bringing “confusion worse confounded” upon biological thought. In the interests of clear thinking I cannot help regretting this unnecessary result, although the spread of the word in the Batesonian sense places me in the

as well as a fuller discussion of the unfortunate confusion into which the subject has been thrown, will be found in the author’s *Darwin and the Origin*, London, 1909, pp. xi.—xiii., 48—51, 258—280.

* Presidential address to Section D. at Winnipeg, 1909.

† *Journ. Genetics*, Vol. II., No. 4, p. 326.

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happy position of the prophet who sees fulfilment even earlier than he expected.

“ A humorist has suggested that the Homer controversy should be settled by a general agreement that the *Iliad* was written not by Homer but by another man with the same name. Those who have heralded with such a flourish of trumpets the profound changes which they assume to be necessary in the Darwinian conception of evolution, may yet save their face by calling the same thing by another name.”*

I now come to details of Professor Punnett's article in the July number of *BEDROCK*, and I here find the irresponsibility already spoken of, the same attitude which seems to be expressed by the words—“ Mendelism is so interesting that it really doesn't matter what one says.” Thus, on page 153, speaking of the inheritance of a small variation, we are told that “ in no clear case has it been shown to exist.” Does Professor Punnett believe that “ family likeness ” is hereditary, or that one element in family likeness, such as the shape of a nose or chin, is hereditary ; that a voice or trick of movement or expression is hereditary ? I do not think that he doubts any of these facts. His statement was just the irresponsible utterance of one who has not thought out the consequences of his own words. And if Professor Punnett still has doubts, at any rate they are not shared by others who are as interested in Mendelian research as he is himself. Thus Professor C. B. Davenport told me in 1909 that he had often been struck with the remarkable persistence of insignificant variations, such as a single small white spot. But leaving the higher animals and coming to butterflies, I had spoken, in the very article † supposed to be criticised by Professor Punnett, of actual evidence in the Hope Collections that “ small features in the pattern of the parent [*dardanus*] certainly tend to reappear in her offspring,” and one such feature was described. Professor Punnett never even alludes to the passage. Nor does he refer to Figs. 11 to 14 in Plate III. of my article, distinctly proving that a small variation in pattern exhibited in the female parent was inherited by all her offspring of the same form (*dubia*). I also mentioned on p. 56 that Mr. Lamborn had sent me another much larger family showing the same hereditary persistence of the same small variation. Of course,

* *Darwin and the Origin*, p. 280.

† *BEDROCK*, April, 1913, p. 50.

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it is possible to argue at some length as to what is "small" and what "large," and I will therefore endeavour to avoid all unnecessary discussion by explaining that the "small" variation, described on p. 56 and shown to be hereditary in Plate III., is just such a change as, in my opinion, formed one of the steps by which a mimetic resemblance was attained. Mr. Lamborn also sent to me, in the early part of last year, two magnificent families of *Hypolimnas dinarcha*, together with their female parents. In one parent the white of the hind wing is faintly tinged with yellow, and there is a very slight difference in the pattern of the fore wing. Both these characteristics, as small or smaller than the "steps" I have postulated, strongly tend to be inherited by the female offspring.

It is, furthermore, easy, by a study of the geographical races of almost any wide-ranging species, to supply the evidence Professor Punnett has failed or not troubled to find. The fine work of the Tring Zoological Museum is chiefly devoted to the comparison, description and illustration of these small hereditary differences between races which, by inter-breeding at the margins of their respective areas, are welded together into a single species. I will illustrate this kind of evidence, of which any amount is available, by reference to one of the species mentioned and figured on Plate I., facing p. 151 of Professor Punnett's paper. The figures of *Danais chrysippus* clearly show the pattern at the tip of the fore wing of average Indian and Cingalese examples. A small white spot is seen lying opposite the lower end of the white bar on the side turned towards the attachment of the wing. This spot, if it were larger and joined to the bar, would make with it an L-shaped marking. When we follow *D. chrysippus* eastward, for example, into the Macao and Hong Kong districts, that spot does become larger and is sometimes joined to the bar. Following the butterfly westward into Africa, the spot disappears altogether, or, when it persists, is smaller than in Professor Punnett's figures. Other minute geographical changes in the same butterfly might be described, and, as I have said, any number in other species. The only question that remains is their transmissibility, but I imagine that Professor Punnett will hardly doubt that each local pattern of a butterfly, occupying corresponding stations in the different parts of its total habitat, is a hereditary pattern. There is really no room for doubt,

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because geographical races, including some forms of *chrysippus*, have often been bred and found to come true.

Professor Punnett—unintentionally no doubt—misinterprets my views as to the first origin of a mimetic likeness in a butterfly with a pattern widely different from its model. More than once he speaks of the “minute initial variation,” or words to that effect: on p. 153 he alludes to “the difficulty of the initial stages, so clearly recognised by Darwin, and so lightly disposed of by” me: on p. 146 he refers to an interpretation based on the theory of mimicry as “altogether too facile.” I am sorry to indulge in a *tu quoque*, but I must point out that it is very easy to meet the difficulty of the origin of a mimetic likeness by assuming that it appeared in its present form. I have never found it light and simple work to attempt to make out these past histories. The careful study of a long series of specimens from many parts of as wide a range as possible is generally required, and after doing one’s best the dominant feeling at the end is often the desire for more specimens from other localities. If Professor Punnett had troubled to study what I have written he would never have spoken as he does about the supposed “minute initial variation.” I have always recognised that the first variation must be something appreciable, something which, at any rate, at a distance and on the wing would recall the pattern of the model. Mimicry is far more characteristic of forest species than of those living in the open, and Mr. C. F. M. Swynnerton has made the reasonable suggestion that the origin of mimicry is facilitated by the alternating light and shade of a tropical forest, where it is easy to confuse patterns readily distinguishable under ordinary conditions of illumination.

In an earlier article in *BEDROCK** I attempted to trace the origin and history of the mimetic pattern of the eastern female of *Acraea alciope*, which resembles the male of one species of *Planema* and the male and female of another. I gave reasons for the belief that the eastern mimicry was started by the sudden appearance of a white bar crossing the hind wing. I furthermore showed that out of 249 western females bred by Mr. W. A. Lamborn in the Lagos district, a single one exhibited “a well-marked white bar crossing the fore wing,” showing “how a mimetic modification might arise

* No. 1, April, 1912, p. 48.

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if an appropriate model existed in the locality.” Concerning the origin of the eastern mimic, the following passage is quoted from p. 63 :—

“ It is probable that by spontaneous variation a white band like that shown in Fig. 13 appeared in the ancestral form (Fig. 12), and that this was from the very first sufficient to confer some advantage by suggesting the appearance of a dominant Model (Fig. 6). From this point Natural Selection acting on further variations produced the detailed likeness which we see in the white band itself and in the other mimetic features.”

I think Professor Punnett will admit that he has given an unfair impression of my views. But it is not only for the purpose of correcting him that I quote rather fully from the earlier article. In writing it I left off as usual longing for more material. Within the past few months the wish has been gratified. The paper was written after a study of the splendid western series sent to me by my friend, Mr. W. A. Lamborn, Entomologist to the Agricultural Department of Southern Nigeria, and the equally splendid material from Eastern Uganda by my friends, Mr. C. A. Wiggins, D.P.M.O., of the Uganda Protectorate, and Dr. G. D. H. Carpenter, Member of the Royal Society's Sleeping Sickness Commission. The eastern females were nearly all perfect mimics of eastern models, but a very few were of the western type, and of these again a small proportion exhibited the incipient but distinct white bar which suggested the origin of the eastern mimetic form. I was especially anxious for specimens from further west, from a zone of country where I thought the transitional forms might be abundant. Owing to the kindness of my friends Mr. S. A. Neave and Mr. Guy A. K. Marshall, Secretary to the Entomological Research Committee of the Colonial Office, I have now had the chance of studying carefully the fine collection made in Uganda by the former as travelling naturalist to the Committee. Mr. Neave not only collected in Eastern Uganda, with results as regards the female *alciope* similar to those obtained by my other friends, but also travelled westward to the Semliki Valley, the western boundary of Uganda. He here entered the margin of the great tropical forest which stretches unbroken to the west coast. Uganda itself is largely open country with patches of primitive forest, doubtless formerly continuous with one another and with the great forest now ending at the Semliki.

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Mr. Neave collected in the Semliki Valley and in forest patches near it. In his whole collection from this part of Uganda there is not a single mimetic female *alciope* of the eastern type: there are many females of the western type, and of these a considerable proportion bear the incipient bar developed to a very variable extent, and sometimes appearing on the under surface alone. Here, then, in the very zone of country where, on the theory of mimicry, we should expect them to be, we meet with the earliest stage of the eastern mimic, but, so far as we know, never the finished product.

I can hardly expect that this evidence will appeal to Professor Punnett, who seems to be singularly impervious to arguments based on geographical distribution. Thus he makes no reference, save one, to the distribution of the mimetic and other forms of *P. dardanus*, although geographical distribution was the strongest part of the argument he was professing to answer. His one reference hardly strengthens his case. He speaks of "wildly assuming that because a form lives on an island it is therefore ancestral" (p. 164). No assumption was made on such grounds. *Papilio meriones* was held to be ancestral, not because it lives in Madagascar, but because the female possesses the non-mimetic pattern of the male. And Professor Punnett, too, when it suits his purpose, is quite willing to base his arguments on the conclusion that the non-mimetic male of a mimetic species bears the ancestral pattern.* Incidentally it may be remarked that it is somewhat humorous for Professor Punnett to speak of anyone wildly assuming anything.

While we are on the subject of *P. dardanus* it will be convenient to correct another mistaken assumption. Professor Punnett begins a paragraph on p. 161: "Let us . . . for the sake of argument, leave out of account the fact that some, at any rate, of these transitional forms (such as *trimeni*) are specific. . . ." *Trimeni*, named by me in 1906,† is not specific, and has never been spoken of as specific by any writer except Professor Punnett in the above-quoted passage. It is a female form existing side by side with other and mimetic

* See pp. 151, 152, of his BEDROCK paper. It is a pity that in Plate I., facing p. 151, in which Professor Punnett illustrates his argument, *D. chrysippus* should be represented by a male in both outer and inner circles, although all the other species are represented by males in the outer and females in the inner circle.

† *Trans. Ent. Soc., Lond.*, 1906, p. 283.

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female forms in the sub-species *polytrophus* and *tibullus* of *Papilio dardanus*. Plate II. of my last BEDROCK article would have shown this clearly to Professor Punnett if he had studied it even superficially ; for seven of the figures are distinctly labelled “ *Polytrophus* male ” and “ 6 *Polytrophus* females of 4 forms,” two of the latter being named “ *trimeni*.” No trouble is necessary in hunting up reference numbers in a description of the figures. All the information is printed on the face of the plate. I think I am entitled to use Professor Punnett’s words on p. 161 and ask for “ a more critical spirit.”

It is difficult to take seriously Professor Punnett’s reply to my criticism* of his statement that, according to the Darwinian view, a certain African Danaine butterfly arose direct but gradually from another, and that, according to the Mendelian, the origin was sudden.† I pointed out that no one had ever suggested such an origin at all, and that those who had studied the group placed the two species rather far apart. Professor Punnett’s reply is curious. The conclusions on the zoological affinities of his group reached by the great Swedish naturalist who has spent most of his life in the exact and careful study of African butterflies he likens to those of Moses, his own conclusions on the same question reached by no study at all, he compares to those of the modern zoologist ! This is the way in which he is concerned to defend an elementary exposition of his subject intended for the non-scientific public !

Returning for a moment to the female *Acraea alciope*, I think that the facts brought forward in the first number of BEDROCK, together with Mr. Neave’s more recent discoveries referred to in the present paper (pp. 302, 303), will convince the great majority of naturalists that the mimetic pattern was attained by steps and not suddenly. Yet the result is here far less elaborate than that seen in the two mimetic females of *Papilio polytes* which Professor Punnett maintains were produced at a single bound. I have never yet written on the evolution of these females, and, since the history as I interpret it is different from that which Professor Punnett ascribes, on pp. 153 and 154, to the followers of the theory of mimicry, it is appropriate that I should do so on the present occasion. I have

* BEDROCK, April, 1913, p. 52.

† *Mendelism*, 1911, pp. 134—5.

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the advantage of writing with several specimens from Ceylon as well as some from other parts of the geographical range beside me—the former collected and kindly given to me by Professor Punnett himself.

Professor Punnett's Plate II., facing p. 153, gives a fair idea of this butterfly and its two models. The reference numbers to the *hector* and *aristolochiæ* forms are unfortunately transposed on p. 153, and on the plate the intense red spots on the hind wings and the same vivid tint on the body of one model, *P. hector*, are invisible, while the dull red spots on the hind wings of the other model, *P. aristolochiæ*, can be detected with difficulty. The photograph required screens, special plates and long exposure to give a good reproduction of these difficult tints, but its failure has a special interest in relation to the present discussion. To the human eye the red of *P. hector* is so aggressively assertive that an æsthete of thirty or forty years ago would have declined to live in the same house with the butterfly; yet, upon Professor Punnett's photographic plate, it produced the same effect as black. The dull unobtrusive red of the corresponding mimetic female would have been tolerated or even welcomed at the period of "Patience"; yet it asserts itself on the plate and comes out in its true value against the black background of the wing. It is evident that the pigments are quite different, and spring from different genetic factors in model and mimic.

Professor Punnett supposes (p. 155) that the two mimetic females arose suddenly in their present form from the male-like female. "After all," he says, "the different females of *polytes* are doing the same sort of thing every day." Men with potential aptitude—more or less—for reasoning are born every day. Does Professor Punnett therefore believe that man as he is now arose suddenly from a common ancestor with the anthropoids? If not, the fact that the different females of *polytes* are produced now is hardly an argument that they were originally produced in their present form. I would ask any thinking naturalist to look at Professor Punnett's Plate II. and compare the two mimetic females (3 and 4) with their two models (5 and 6) and with their non-mimetic ancestor (2), to note carefully the various points of resemblance to the models and of difference from the ancestor—points analysed on pp. 308—10, and

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then consider whether it is reasonable to suggest that all these features in the pattern—some of them detailed and nearly exact, such as the V-like white marks near the apex of the fore wing in the “*hector* form” (3)—that all these arose suddenly and together in each of the two mimics. That a large variation may arise suddenly no one ever doubted, but not many naturalists will accept the view that a complex pattern of many elements resembling the corresponding elements in an entirely different species could spring into existence as a whole and complete in all its details.

Granting the sudden origin of the two mimetic forms, Professor Punnett admits, on p. 155, that they would be preserved and rendered predominant by Natural Selection, but it is difficult to reconcile this part of his paper with pages 156 to 158, in which he reaches the conclusion that the proportion of the mimetic females in Ceylon expresses a Mendelian equilibrium undisturbed by selection. *Papilio polytes* has a wide range in the Oriental Region. Over most of this range it is accompanied by one model only, and not two; in certain localities this single model is so scarce that it is impossible to believe that it can act as a model at all. With these facts, which enable him to ascertain what actually happens in the absence of one or both models (as effective agents), Professor Punnett light-heartedly chooses Ceylon, where both models are common, as his crucial locality, and, entirely neglecting comparison with other areas, concludes, with all the emphasis of italics, that “*Natural Selection is non-existent in so far as concerns the relation of the mimetic to the non-mimetic females of Papilio polytes*” (p. 158).

Now let us see where the facts lead. *Papilio hector* is only found over a part of the area of *polytes*, and of the second model *aristolochiæ*. Localities in this part, Ceylon being one, yield both forms of mimetic female. Localities in the area outside this part yield one mimetic female, the “*aristolochiæ* form.” The species forms an interbreeding community, at any rate over the continental part of its range, and it is to be expected that a certain small proportion of “*hector* females” will stray into the country outside the boundary of their model. I only suggest this probability from an experience of *dardanus* and other mimetic species in Africa. In the Hong Kong and Macao districts *P. hector* is unknown, and so is its mimic: *P. aristolochiæ* is excessively rare, so much so that some

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observant naturalists long resident in these localities have never seen it at all. *Papilio polytes* is, according to these naturalists, the commonest or one of the two commonest swallow-tails of the locality. Here then is a splendid opportunity for Mendelian equilibrium. What we really find is the almost complete preponderance of the male-like female. I have lately received six females—all of this form—captured by Captain R. A. Craig on Stonecutter's Island, in Hong Kong Harbour. Not a single model was present in the collection. Dr. Seitz, in a long experience of the Kowloon district, never saw any other form of female and never saw the model. Commander J. J. Walker alone thought that the "*aristolochiæ* form" was as common as the non-mimetic form at Hong Kong, although he, too, never saw the model. Mr. J. C. Kershaw's experience at Macao corresponds with that of most observers at Hong Kong. He finds the male-like female of *polytes* is the common one and has never seen *P. aristolochiæ*.* The opposite condition is found in New Guinea, where the representative of *polytes* has but a single female form mimetic of the representative of *P. aristolochiæ* and the male-like form is unknown.

In order to reach safe conclusions we really need many cabinets filled with specimens of this butterfly and its models from localities scattered over representative parts of the range. Many thousands of specimens are required. But we already know enough to feel confident that the two mimicking females only occur regularly where the two models are common, and that when one model is absent and the other common, the corresponding mimetic female is common; finally that when the single model is wanting or extremely rare the corresponding form is absent or rare. The facts do not warrant Professor Punnett's italicised conclusion quoted on p. 306.

I will now attempt to trace the evolution of the two mimetic females of *polytes*. I do not believe for a moment that the species is palatable to insect-eating animals in general. The under-surface pattern of the male closely resembles its upper surface, only differing in that it is rendered even more conspicuous by the larger yellow marginal markings on the hind wing as well as by a row of red spots lying within these markings. Such a relationship between the

* See *Proc. Ent. Soc. Lond.*, 1913, pp. xxxi., xxxii., where observations in the Hong Kong and Macao districts are recorded and references given.

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upper and under surface is also found in *P. aristolochiæ*, and is very characteristic of the groups which supply the best-known models for mimicry. It is the very opposite of the relationship seen in butterflies with a dead-leaf-like or otherwise procryptically-coloured under-surface to the wings. The mimicry is, I hold, Müllerian, and the mimetic forms have merely exchanged the warning patterns peculiar to their kind for those characteristic of two other far more distasteful species with a more flaunting and slower flight. An exchange like this of one conspicuous pattern for another, when it can be established, seems to me a good criterion of Müllerian mimicry. We should expect a Batesian mimic to be developed out of a species with a procryptic under-surface. Professor Punnett accepts without question Haase's hypothesis that the distasteful qualities of the models are derived from the food-plant. Haase may be right, although I have always felt that stronger proof is required, but under any circumstances distasteful qualities can be elaborated in the body and are not necessarily borrowed direct or with slight change from the food-plant. Commander Walker has told me of the larva of the Australian *Papilio macleayanus*, feeding on the "Sassafras tree," *Atherosperma moschatum*, which emits from the well-known pair of glands behind the head a "strong and very disagreeable scent"—which is "totally unlike the pleasant nutmeg-like fragrance of the Sassafras, but resembles that of butyric acid or the smell of the little malodorous ants of the genus *Crematogaster*."* Commander Walker even found that the caterpillars were more easily collected by smelling for them than by looking for them. A citronaceous food-plant is not evidence of the palatability to insect-eaters of *P. polytes*.

We now come to the transformation of the non-mimetic into the mimetic forms. Professor Punnett assumes (pp. 153, 154) that "on the theory of mimicry" the two forms were evolved independently; but I do not think there is the slightest doubt that the mimic with a far wider range, the "*aristolochiæ* form," was evolved first and that later on the "*hector* form" was developed from it and not direct from the male-like female. The essential and first change, upon which the detailed likeness to *P. aristolochiæ* has been built up, was, I do not doubt, the shortening and widening of

* *Ent. Mo. Mag.*, xli. (1905), p. 220.

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the yellow bar crossing the hind wing of the female *polytes*. The bar is not only widened by the lengthening of its central constituent spots, but by the appearance of a patch of yellow at the end of the cell. A very similar shortening and widening of a yellow bar crossing the hind wing is to be seen in an African Nymphaline butterfly, *Neptis woodwardi*.* The mimetic transformation is here evidently very recent, and distinct progress is seen† when we pass from the N.E. shores of the Victoria Nyanza to the Kikuyu country, east of the Rift Valley, where the Danaine model (*Amauris albi-maculata*) is especially predominant, and other mimics of its pattern abound.‡ Such a change in its most conspicuous element would by itself cause the pattern of *polytes*, upon the wing or at a little distance when at rest, to suggest that of *aristolochiæ*. The remaining features of the resemblance were then gradually added, each contributing something to the effect and suggesting more and more strongly the pattern of *aristolochiæ*: (1) the disappearance of the marginal yellow spots of the fore wing, (2) the emphasis and reproduction, on the upper surface, of the sub-marginal spots of the hind-wing under surface—already present in the male and generally red, although sometimes yellow, already tending to appear on the upper surface of some male-like females; (3) the peculiar light-and-dark striation of the outer half of the fore wing, and its reproduction with a marked brightening of the pale elements on the under surface; (4) lastly, the almost entire disappearance from the hind-wing upper surface of the yellow lunules marking the bay-like indentations of the margin—a character already extremely variable in the male and male-like female. I do not mean to imply that these changes took place in the above order or that none of them occurred simultaneously. Comparison with the “*hector* form” renders it probable that (4) was the last change (see p. 310).

Now that the elements in the resemblance to *P. aristolochiæ* have been analysed, the improbability of their all appearing together at the same moment is emphasised. That Mendelian heredity has probably played an important part at some of the stages I freely admit. Why Professor Punnett should prefer to think that

* *Trans. Ent. Soc. Lond.*, 1908, p. 512.

† *Ibid.*, Pl. XXIX., Figs. 2 and 4.

‡ *Ibid.*, Pl. XXVIII.

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the Mendelian principle can only act once in the history of a mimetic form I am at a loss to imagine. Some mimetic transformations are simple, some are excessively complex; he seeks to explain them all by a single variational leap. What reason has he for thinking that variational activity—whatever may be its unknown cause—like certain flowers, can only bloom once? Why should he seek to lay this hard burden on the Mendelian principle as a factor in evolution? This question is raised at the present point by the remarkable contrast between the simple evolution of the “*hector* form” and the complex transformation I have attempted to describe in the preceding pages. As regards the hind wing, the “*hector* form” possesses almost precisely the pattern of the “*aristolochiæ* form” with its yellow transformed into red—a change which may well have occurred suddenly. The comparison between Figs. 3 and 4 on Professor Punnett’s Plate II. shows the nature of the transformation, but to appreciate it fully the actual specimens should be studied. The marginal and sub-marginal lunular markings are larger in the “*hector* form,” and this is the only constant difference between the hind-wing patterns of the two forms. As regards the marginal lunules it is probable that the “*hector* form” arose before these markings had become evanescent, as they now are on the upper surface of the “*aristolochiæ* form.” These markings—although out of place in a mimic of *P. hector*—are red like the rest of the hind-wing pattern in the “*hector* form,” a probable indication that the change to red was a single transformation, involving some divergence from the new model, although, upon the whole, resemblance to it. At the same time the likeness is a rough one, for, as I have said, the hind-wing pattern, apart from its colour, is that of the “*aristolochiæ* form” and its model. The fore-wing pattern is doubtless the most conspicuous part of the “*hector* form,” and here the likeness to the model is far more convincing. It has obviously been produced from the striated fore wing of the “*aristolochiæ* form” by reducing certain parts and emphasising others, on both surfaces, and, upon the under, distinct traces of the increased paleness of the older form are retained on parts of the wing that are black in the model, *P. hector*.

How can we account for the evolution of two mimetic forms in a butterfly which remains dominant when its models are absent or

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excessively rare? It is worth while to consider this question in some little detail, for I believe that the true explanation is different from that usually given.

Papilio polytes is an unusually dominant and successful swallow-tail. Its rate of reproduction, combined with a probable measure of distastefulness advertised by a conspicuous pattern, its powers of flight, alertness, and other adaptations of many kinds, keep up the large average numbers in spite of the attacks of enemies of all sorts in all the stages of its life-history. The large numbers that survive in every generation will, of course, include the fittest, and so the high level of protective efficiency is maintained. This is the condition of *polytes* in the Hong Kong and Macao districts where the single model is so rare that it is unreasonable to suppose that it exerts any effect, and this was doubtless its condition before the evolution of the mimetic forms. There is no reason to suppose that the surviving percentage of *polytes* was increased by the presence of the *aristolochiæ* model or during the growth of the mimetic likeness. All that happened was this: certain variations formerly unselected, now tend to fall into the surviving percentage, and, once started, the further stages of transformation were effected in the same way. Each change that suggested still more strongly an advertisement common to a far more distasteful form would tend to be selected. So, too, when *polytes* spreads beyond the range of *aristolochiæ*, or when the model for some reason disappears from an area in which *polytes* is abundant, the constitution, not the amount, of the surviving percentage is changed. The mimetic pattern soon disappears, although the species that bore it remains as abundant as before. The survival or extinction of the species is not affected: all that has happened is the survival or extinction of a pattern borne by a certain proportion of the individuals of the species. When these disappear other individuals with another pattern take their place. It is, furthermore, extremely probable that selection is reversed when the models are absent, for a female that resembles the male is better advertised than one which resembles a non-existent model. Although I believe that many mimicking species bear the above-described relationship to their models, I do not mean to imply that this is always so. No doubt there are plenty of mimicking species which depend upon the presence of the model for their

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existence and could not live in areas from which the model disappeared.

I have answered the main points raised by Professor Punnett, and should have been glad of the opportunity of discussing them all, but it seemed better to devote a considerable part of the present article to *Papilio polytes*, and thus offer what a Darwinian really believes as a substitute for what he is assumed to believe.



Broadhead.