



THE EVOLUTION OF MIMETIC RESEMBLANCE

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

IN my last article in the October number of *BEDROCK* I found it necessary to devote the greater part of the available space to an issue that had been raised by Professor Punnett—the inheritance of small variations. This was an issue so tremendous that the immediate controversy on Mimicry became by comparison insignificant, and I had the less hesitation in cutting it short because I had already written elsewhere on the questions put by Professor Punnett. He now suggests that some of these questions were unanswered in my last article because I had no answer to give. I will, therefore, put his points *seriatim* in the forefront of the present article, summarising under each the answers that have already been given and including new evidence when such is available.

(1) The theory of mimicry “confers upon minute variations a selective value which is inconceivable when regard is had to the nature of the selecting agent.” To most naturalists it is not only conceivable, but even certain, that many kinds of birds can see as well as or better than man. I have published some evidence on this subject in the *Proceedings of the Entomological Society of London* (1912, pp. liii—lv). That the sight of man can easily appreciate the “minute variations” alluded to by Professor Punnett is proved by an example published on p. cxxxviii of the same *Proceedings*. The evidence is so interesting that I will quote it in full. Dr. G. D. H. Carpenter wrote to me, September 21st, 1912, from Bugalla, one of the Sesse Islands, in the north-west of the Victoria Nyanza :—

“I caught a very nice *initial variety* of *Ps. terra* the other day. It had a very slight yellow suffusion of the black ground-colour

BEDROCK

along the costal margin of the forewing, and the black bar between the sub-apical and hind-marginal tawny areas was slightly thinned away. This specimen, however, *looked distinctly different*, both at rest and on the wing, which tends, I think, to show how the smallest variations may have selective value. This is always rather a stumbling block, so it was nice to see it actually exemplified."

Dr. Carpenter alludes to this and other small variations of the same mimetic pattern in this journal for October, 1913 (pp. 360—1),* bringing them forward, in fact, as an answer to this very objection. The butterflies referred to by Dr. Carpenter may be studied by any naturalist in the Oxford University Museum. They are good examples of those "minute variations" which, as I believe, have provided the steps by which mimetic resemblance has been attained.

(2) The theory of mimicry "makes the sweeping assumption that such minute variations are inherited." In answer to this objection I gave, on pp. 299—300, several examples of the inheritance of small variations, most of which are passed over in silence by Professor Punnett. I asked if he believed "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 gave examples of such inheritance in mimetic butterflies, described and illustrated in earlier papers, and said that he had never even referred to them. In his latest paper he still neglects them. I shall have more to say about the one example, *Danaida chrysippus*, that he attempts to explain as the result of climatic influence. In the meantime there is one piece of evidence brought forward in my last paper which has so important a bearing on this very question that I venture to refer to it again. I spoke on pp. 302, 303, of the geographical changes in the females of *Acræea alciope*, showing that "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." These early stages were found in western, the finished product in eastern Uganda,

* All pages quoted without indication of the original source refer to BEDROCK for October, 1913.

EVOLUTION OF MIMETIC RESEMBLANCE

but accompanying the latter is a small percentage of the early stages. A single example (Fig. 13, facing p. 62 of *BEDROCK* for April, 1912) was even captured by Dr. Carpenter on Damba Island in the Victoria Nyanza. It is, therefore, impossible to explain the difference by an appeal to climate; for the abundant finished product and the rare early stages—representing different levels of development—fly together in the same forest patches in eastern Uganda and have often been caught on the same day. The patterns are clearly hereditary and not caused by climate; the differences are small, and together they bridge over the gap between the western female which mimics the males of western *Planemæ* and the eastern female which mimics the male of a Uganda *Planema*.

(3) The theory of mimicry “is driven to argue for an utterly unknown and mysterious process by which these minute variations can be built up into a widely different and fixed form.” This objection seems to be in large part a rhetorical re-statement of the first. The “unknown and mysterious process” is Natural Selection, its agents, insect-eating enemies, chiefly and perhaps exclusively birds. That minute variations are, as a matter of fact, “built up into a widely different and fixed form” we can see for ourselves by tracing the females of *Acraea alciope* from the Semliki Valley into Eastern Uganda.

(4) The theory of mimicry “is unable to account for the absence of transitional forms when the germ-plasms of the old form and the new one are mixed.” I explain the segregation that occurs by the Mendelian theory, which, I believe, as stated on pp. 309—10, has played an important part in the evolution of mimicry, and especially of those examples in which the females appear in two or more different forms. I find no difficulty in believing that the Mendelian principle operates at many successive stages in the evolution of such resemblances, and I asked Professor Punnett why he preferred to think that it can only act once in the history of a mimetic form, and why he sought to lay this hard burden on the Mendelian principle as a factor in evolution (p. 310). He made no reply.

Within the last few weeks I have received from Mr. W. A. Lamborn a family of *Papilio dardanus* bred from a captured *hippocoon* female. While Mr. Lamborn's six previous families from the same parental form, also from Southern Nigeria, yielded no females except *hippo-*

BEDROCK

coon, this last includes six *hippocoon* and eight *dionysus*—a strange ancestral non-mimetic form scattered in relatively small numbers along the tropical west coast. The most probable interpretation of the facts is the assumption that *dionysus* is dominant over *hippocoon* and that the male parent was a heterozygote. Mr. Lamborn exposed some of the pupæ to cold, but this does not explain the fact that all six *hippocoon* are extremely constant, while the eight *dionysus* exhibit the most remarkable variation. *Hippocoon*, on the west coast, in the presence of the predominant model *Amauris niavius*, is abundant, and presents, in spite of minute variations which are hereditary, a nearly constant pattern. *Dionysus*, without a model, is rare and excessively variable. The contrast in nature is repeated in the offspring of a single family. It is probable that results of the same kind, but even more striking, will be obtained when *trimeni* is bred on the Kikuyu Escarpment. Professor Punnett implies that, in speaking of this latter form as “specific,” he did not claim for it specific rank, but merely meant that it was fixed and definite. I am glad to know his meaning, for the passage misled me as well as other readers. *Trimeni*, however, is remarkable for its want of fixity, and especially for variations which form a transitional series towards the male-like female on the one hand and the *hippocoon* pattern on the other.

(5) The theory of mimicry “has no adequate explanation to offer for the frequent absence of mimicry in the male sex.” Wallace originally explained this absence by the probable hypothesis that mimicry is of more value to the female, and therefore more stringently selected in this sex, than in the male. Darwin argued that this hypothesis is by itself insufficient; for why should not the advantage gained by the female be transferred to the male?—“It would be some advantage, certainly no disadvantage, for the unfortunate male to enjoy an equal immunity from danger.” Darwin continued: “For my part, I should say that the female alone had happened to vary in the right manner, and that the beneficial variations had been transmitted to the same sex alone.” The answer to-day is the same as that given by Darwin and Wallace. Predominant female mimicry is due to the fact that the sex-limited colours and patterns of females are more variable than those of males, and thus more frequently supply the material for selection.

EVOLUTION OF MIMETIC RESEMBLANCE

A more stringent selection operates upon more varied material. The variations, being linked with sex, are not transferred to the male.*

(6) The theory of mimicry "leaves without any solution those numbers of cases of polymorphism where there is no question of mimicry." It is unreasonable to suggest that variations which are not mimetic ought to be explained by the theory of mimicry. Neither this theory nor the parent theory of Natural Selection explains variation. It is the other way,—hereditary variation is one chief explanation of Natural Selection and of mimicry. Although we do not know the cause, it is the fact that female butterflies are far more subject to polymorphism in colour and pattern than the males, thus supplying material upon which female mimicry may be built up.

(7) Lastly, the theory of mimicry "endows birds with powers of selective destruction which are certainly not deducible from the available evidence." This objection again is simply the first expressed in different language. I may say, however, that I have never claimed that the direct evidence warranted any such conclusion. It is hardly likely, I think, that such direct evidence will ever be forthcoming, although I hope for the best, and shall not cease to stimulate observation on this special point. We have already a large body of direct evidence that insects with warning colours are distasteful to the majority of insectivorous birds, and that procrystic species are palatable to them. We may reasonably hope for an immense increase in this evidence. There is also some evidence that enemies are misled by mimetic resemblance, and that they remember an unpleasant experience and associate it with the appearance of the object from which it was received. On these lines, too, it is reasonable to expect far more evidence. But I do not think it likely, although of course it is possible, that there will ever be available *direct* evidence of the growth or maintenance of mimetic likeness by means of selective destruction. There is already a great mass of indirect evidence which is increasing at a very rapid rate. I allude to such observations as those of Dr. G. D. H.

* This question is more fully discussed in *Darwin and the Origin*, 1909, pp. 132—9, where the above quotations from Darwin's letters are given at greater length.

BEDROCK

Carpenter, published in the October number of *BEDROCK* (pp. 359—60)—the fact that the mimetic forms of a polymorphic *Pseudacraea* vary more freely and run into each other more completely on islands in the Victoria Nyanza, where their models are relatively scarce, than they do on the mainland, where their models are abundant. How interesting is the comparison between these observations in Uganda and those referred to on pp. 36, 37, as made by Mr. W. A. Lamborn in Southern Nigeria, where two female forms of *Papilio dardanus* were bred in a single family; one of them, *hippocoon*, with an abundant model on the west coast—constant; the other, *dionysus*, an ancestral non-mimetic form—extremely variable. The same difference exists between the wild forms, as may be seen in any good collection from the west coast. No cause, except selection, has been suggested for the relative rarity and variability of the non-mimetic form as compared with the abundance and constancy of the mimetic, and the same comparison holds between *trimeni* and the fully developed mimetic forms of East Africa. Indirect evidence along these and other lines is, as I have said, accumulating steadily and rapidly, and will probably convince the great majority of naturalists.

I now propose to deal with other issues raised by Professor Punnett in his last article.

Of course I agree that “Charles Darwin’s work is not beyond fair criticism any more than that of any other man.” Weismann’s contention that “acquired characters” are not transmitted was a criticism of Charles Darwin’s work, and I endeavoured, with others, to introduce it to English zoologists. But this new contention, as it was then, had been investigated with the utmost care and was supported by evidence on the most varied lines. How utterly different is the spirit of Professor Punnett’s rash and unsupported assertions. The hereditary transmission of small variations plays an infinitely more important part in the Darwinian theory of evolution than the principle against which Weismann developed his carefully planned and elaborate attack. And Professor Punnett is content to sweep the whole fabric aside without evidence, without critical examination. The dogmatic statement that the inheritance of minute variations is a “sweeping assumption” does imply that either Darwin or the speaker is a hasty generaliser; and it is well to

EVOLUTION OF MIMETIC RESEMBLANCE

create prejudice against the attempt to settle tremendous issues in this offhand manner.

I pointed out in 1909 that Professor Bateson and Professor Punnett had misinterpreted de Vries to English readers, the former even stating that the Dutch botanist makes a "clear distinction" between "fluctuations" and "mutations"—"clear" forsooth, when the language used was so much the reverse of limpid as utterly to mislead the exponent himself! Until Professor Punnett's last article, in *BEDROCK*, published in January of the present year, I have seen neither defence nor admission of error on the part of these two exponents of de Vries. Now, however, Professor Punnett does admit that he "may have erred," but maintains that, although de Vries does not make the distinctions he had imputed to him in a popular work intended for general readers—still the distinctions were those which de Vries ought to have made! Indeed, so strongly does Professor Punnett feel this that he tells us he is going to continue to use de Vries' terms, not in the sense in which de Vries uses them, but in that which he wrongly attributed to de Vries. How useful these words will be, and what an aid to clear thinking, in the controversies of the future!

Professor Punnett supposes that I maintain de Vries' "fluctuations" to provide the variational steps by which mimicry was brought about. I stated in the October number (pp. 297, 298) that de Vries' "fluctuation" and "mutation" were the same as Galton's "regressive" and "transilient variation." The "fluctuations" or "regressives," if they exist at all, are clearly not the steps of evolution as they were imagined by Darwin or by the Darwinian to-day. Galton at one time maintained, and de Vries now maintains, that the advance which can be made by these steps soon reaches its limit. The small evolutionary steps on which Darwin relied are the very same variations which some writers would now seek to call "Mutations," as if they were something "new and strange"—variations which Weismann showed to be germinal in origin, and therefore called "blastogenic." These furnish the steps of evolution everywhere, including, of course, the production of a mimetic likeness. When selection ceases, the likeness is soon blurred and, finally, obliterated by the appearance of other germinally caused variations that are no longer eliminated.

BEDROCK

I now turn to Professor Punnett's argument that, because the seasonal forms of certain butterflies are capable of being evoked by certain stimuli, the small differences between sub-species or geographical races may be "acquired" by climatic influence. But the former examples were first known to be seasonal because of the times at which they appeared. The latter, too, may differ in their response to seasonal stimuli, but they also differ in other features that appear independently of climate, even when the seasons differ as greatly as in Africa.

Much of the best systematic work of the present day consists in the establishment of these very geographical races, generally distinguished by small differences, but keeping true to their locality. If sub-species are real, then minute variations must be inherited. Professor Punnett suggests that they are unreal. "It seems to me not at all unlikely that the differences are what are often vaguely termed climatic," he says of the local changes in the average size of a spot in *Danaida chrysippus*; and he must hold the same views for all other small geographical variations if he is to maintain the position that no clear case of such inheritance has been proved to exist. I should have thought that he would have spent many years in breeding experiments before he thus ventured to sweep away the foundations of so much good work. But this is not the method of the present-day writer on evolution. Johannsen weighs beans, de Vries records the variations of Evening Primroses, and instantly, without any further effort, without even troubling to read de Vries himself accurately, the whole foundations of evolutionary thought are assumed to be broken up.

Now that the question has been raised, it will doubtless fall to my friends to make the experiments which will test whether sub-specific characters are real or unreal. Indeed, I have already written to several naturalists on the subject.

In the meantime, there are very strong reasons for rejecting Professor Punnett's suggestions that these local differences are climatic. The fine butterfly *Danaida plexippus* (*archippus*), known in North America as the "Monarch," is a close ally of *D. chrysippus*. It extends through nearly the whole of the American continent, splitting up into at least three geographical races, one in North America, two in the South. There is reason for the belief that it

EVOLUTION OF MIMETIC RESEMBLANCE

was originally an Old World butterfly, and that it reached America by way of the north. It has at any rate inhabited North America long enough to have produced an exceedingly perfect mimic, while it has wrought no such effect in the South. In spite of its long sojourn in the New World, its pattern still strongly resembles that of its Old World allies. Nevertheless, it has formed geographical races, distinguished from each other by small differences of pattern.

During the past seventy or eighty years this butterfly, probably aided by steam transport, has been spreading to many parts of the Old World, both west and east of America. Commander Walker, who has made a special study of the subject, has kindly furnished me with the dates at which it was first recorded from the following localities :—

First westward : New Zealand, 1840 ; Marquesas Islands, “ about 1860 ” ; Sandwich Islands, 1845 — 50 ; Caroline Islands, 1857 ; Tonga, 1863 ; Niuaufou, 1866 ; Samoa, 1867 ; Tonga Tabu, 1868 ; Rarotonga, 1869 ; Tahiti, 1870 ; Lord Howe Islands, 1870 ; Clarence River, N.S.W., 1871 ; Melbourne, 1872 ; Queensland, 1870 ; Solomon Islands, 1887 ; New Britain, 1895 ; Hong Kong, 1896 ; Straits of Malacca, 1889.

Next eastward : Azores, 1863 ; Canary Islands, 1893 * ; British Isles, 1876 ; France, 1877 ; Atlantic Ocean (200 to 300 miles from the British shore), 1880 ; Atlantic Ocean (sixty miles from Cape St. Vincent), date ? ; Gibraltar, 1886 ; Grecian Archipelago, 1897.

In many of these localities the butterfly has established itself, and is now apparently a permanent resident. In spite of the great climatic differences to which it has been subject in the course of this extensive colonisation, Commander Walker has never seen a record of any except the North American form. The natural inference is that the species is not sensitive to climatic conditions, and that the South American races are not due to this influence.

The eastern and western sub-species of African butterflies nearly always meet and interbreed in eastern Uganda or western British East Africa. How can climate explain the phenomena that are manifest at their overlap—either an abrupt replacement, or, probably

* The butterfly certainly reached the Canary Islands much earlier than 1893. I saw it myself in Grand Canary in 1888.

BEDROCK

more often, a series of transitional variations? Furthermore, in *Danaida chrysippus* itself, although there is a marked geographical difference in the average size of a certain white spot on the forewing, yet in the same locality and at the same time, these spots are seen to vary greatly in size.

Professor Punnett says that he is not prepared to subscribe without reserve to the view that the female of *Elymnias undularis* was originally like the male. He does not discuss, and is probably not aware of, the evidence—very old and well known—which makes this conclusion probable. I remember exhibiting illustrations of the following series in an evening lecture before the British Association in 1890.

A little group of Oriental species and sub-species of *Elymnias*, of which *undularis* is one, presents us with the following sequence: (1) in the Andaman Islands, both sexes alike and resembling all the other non-mimetic males of the group, including *undularis*; (2) in Sikkim and North-East India, also in Ceylon—female mimetic, male non-mimetic; (3) in Burma—female often with white hind wings in mimicry of a Danaine model with white hind wings, male non-mimetic; (4) in South India—female mimetic, male with a pattern intermediate between that of the female and the non-mimetic male of other localities.

Such a sequence will satisfy most naturalists that the hypothesis doubted by Professor Punnett is the only one consistent with the facts. I am very far from denying that in some cases of sexual dimorphism, the male form may be the more recent, but, so far as I am aware, in all examples with mimetic females, the evidence—whenever evidence is available—points in the same direction as that furnished by *Elymnias*. Thus the facts known concerning *Papilio polytes* will be admitted by most naturalists to support the same conclusion. The females are not, as Professor Punnett implies, constant and invariable. They vary greatly in the same locality, and still more in the different parts of their geographical range. The male pattern is far more constant, although it too undergoes recognisable geographical changes. Furthermore, it is not only more constant than the female, but it resembles the pattern of other allied species. Such resemblances between species have hitherto been accepted as evidence of descent from a common ancestor. In other

EVOLUTION OF MIMETIC RESEMBLANCE

words, patterns like those of the male *polytes* have been regarded as ancestral, as compared with their females, which, diverging in various directions, resemble the patterns of remote species. In the most eastern part of the range on the Asiatic mainland, the *aristolochiæ* models are distinguished by the small size of the white patch on the hind wing. The mimetic females follow them. In Borneo and Sumatra *aristolochiæ* is represented by *antiphus*, without any white spot. The mimetic females follow them, although a small trace of the spot is present in some individuals.

In BEDROCK for last October it was argued (p. 309) that the red submarginal spots of the mimetic females were derived from those already present on the under, and occasionally on the upper, surface of the non-mimetic male. I have lately re-studied this question with a much larger series of individuals and have found additional evidence pointing to the same conclusion. One spot in the series—that below vein 4—is nearly always much smaller than those on either side of it and sometimes it is altogether wanting when they are present. This relationship is commonly found on the under surface of the males and male-like females, and on the upper surface also, when these spots are present,—as they are far more commonly in the male-like females than in the males. The same relationship is also common on both surfaces of the *polytes* females as well as of other mimetic female forms. It is less often seen and less striking in the *hector* form (*romulus*) than in the *polytes* form from the same locality, corresponding with other evidence, based on the evolution of the pattern, which indicates that the former is further removed from the ancestral appearance of the male than is the latter.

I have never contended, as Professor Punnett asserts (p. 571), that because the difference between the patterns of the mimetic and non-mimetic females of *polytes* is “somewhat complex,” it cannot have arisen as a single mutation. I grant that a large and complex variation may arise. Professor Punnett passes over the real improbability—the sudden origin of a complex pattern which matches that of another and remote species. The same difficulty is encountered by the hypothesis that the mimetic females of *Elymnias* arose suddenly.

We know that the mimetic and non-mimetic females of *polytes* are produced without intermediates, and the question is whether

BEDROCK

they developed by a series of stages or suddenly arose in their present form. In the course of this discussion, Professor Punnett triumphantly pointed to the admitted fact that they do so arise! It was this mode of argument that I ventured to parody in a travesty taken too seriously by Professor Punnett.

I stated in October, 1913, that I had always recognised that the first variation which initiates mimicry must be something appreciable, and proceeded to prove it by quoting a striking example from my article in *BEDROCK* for April, 1912. I even complained, and justly, that Professor Punnett had altogether misrepresented me. The only reply that he now makes is triumphantly to assert that the views expressed and illustrated in April, 1912, were "elicited" by his article in July of the following year. I suppose he will now claim that the earliest statement of the kind I remember to have made *—in 1890—was elicited by him!

There is nothing inconsistent between these views upon the origin of mimicry and the passage quoted from *Darwin and the Origin*, by Professor Punnett. I do not regard the "first colour change" which started mimicry as a large variation, or one that differs from the steps of evolution as Darwin postulated them.

I am reminded, by Professor Punnett's particoloured rabbits, of the hooded rats figured by Professor W. E. Castle (*Heredity and Eugenics*, Chicago, 1912, p. 58). Here is a Mendelian investigator who has been led by his experiments to believe that "Mendelizing characters can be modified by selection," and I bring this article to a close by quoting part of the concluding paragraph of his lecture:—

"Accordingly we conclude that unit-characters are not unchangeable. They can be modified, and these modifications come about in more than a single way. Occasionally a unit-character is lost altogether or profoundly modified at a single step. This is mutation. But more frequent and more important, probably, are slight, scarcely noticeable modifications of unit-characters that afford a basis for a slow alteration of the race by selection. . . ."

* *Nature*, October 2nd, 1890. Reprinted in *Essays on Evolution*, 1908, p. 376.

