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On Müllerian Mimicry and Diaposematism.

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XXIII. *On Müllerian Mimicry and Diaposematism.* A Reply to Mr. G. A. K. Marshall. By F. A. Dixey, M.A., M.D., Fellow of Wadham College, Oxford.

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In dealing with my friend Mr. G. A. K. Marshall's most interesting paper (Trans. Ent. Soc. Lond., 1908, pp. 93–142), a large part of which consists of strictures upon views which have from time to time been put forward by me, I have in the first place to thank him for the courtesy which allowed me to become acquainted with his criticisms before these had been laid before the Society. I should wish also to say at the outset that I am sincerely glad that these criticisms have been offered. A theory is not likely to meet with much acceptance until it has been well scrutinised, and has run the gauntlet of adverse comment. The propounder of a new idea ought to welcome any fair objection that can be brought against his views. The worst fate that can befall him is to be passed over in silence; and even if the attack upon his position should prove successful, he has the satisfaction of knowing that at least he has helped to stimulate enquiry, and that the cause of truth has been the gainer. There is a reason for which Mr. Marshall's objections are specially welcome. We are likely to get from him as good a statement of his side of the question as can be made, and if so doughty an antagonist can be successfully answered, it is not likely that the theory which he impugns will have to meet any more formidable attack.

Let me now see what points I have in common with Mr. Marshall, and where exactly we diverge.

In the first place, it is clear that he may be claimed as a believer in Natural Selection and in the principle of Mimicry, both in the Batesian and Müllerian sense. With regard to the latter his words are: "There can be little doubt that a good many cases of mimicry originally adduced in support of Bates' theory must now be explained on Müllerian lines" (p. 93). So far I am quite in accord with him. Moreover, when he says that "the universal application of this latter principle to butterflies . . . seems open to some serious objections" (*ibid.*), I can still give my assent. I have always held that there was room for both theories, which are complementary rather than contradictory. But having said so much, he proceeds to impose very serious limitations on the scope of Müllerian assimilation, and in especial to disallow the conception of what has been called Diaposematism or Reciprocal Mimicry, "even as a mere working hypothesis."

Here he no doubt expects me to join issue with him, and I shall not disappoint his expectation. I maintain, on the contrary, that the operation of the Müllerian factor, though not universal, is a good deal wider than he is disposed to admit; and that the principle of Diaposematism, which, as he rightly says, is a corollary of the Müllerian theory, affords the best explanation that can at present be given of certain interesting cases of mimetic grouping. This, I think, is a fair statement of the issue between us.

The General Argument.

The opening paragraphs of Mr. Marshall's paper contain a fair and lucid presentment of the Müllerian theory. On these passages I have naturally no criticism to offer, though it may be worthy of notice, in passing, that while the fact that young insectivorous animals have to undergo an education in the matter of suitable provender is, as Mr. Marshall says, "sufficiently well established by now" (pp. 94, 95), we cannot eliminate the operation of inherited instinct from the general relation of animals to their food. The avoidance of poisonous fruits, for instance, must, it would seem, be due to an instinct which has grown up under the influence of natural selection. This point, however, though it is well to bear it in mind, is immaterial for present purposes.

The first of Mr. Marshall's assertions that I should question is his statement on p. 95 that the initial mimetic variation must gradually replace the original form. It is hard to see why this must necessarily be the case. The original form may quite conceivably continue to be able to maintain itself, even after it has given rise to a variation which is also capable of a separate existence. Innumerable instances of this persistence of an ancestral form are known throughout organic nature, and indeed they are common enough among the special subjects of our present study.

The variation simply fits into a new place, leaving its ancestral stock to keep on in the old one.

Mr. Marshall goes on to point out (p. 96) that "the mental attitude of the enemy towards its prey has an important bearing upon the results which its attacks will produce." Upon this statement, which is no doubt true enough, he bases the conclusion that "those enemies which have a comparatively low degree of intelligence, and which therefore require to make many experiments . . ." operate more efficiently as producers of Müllerian mimicry than those enemies whose superior intelligence enables them to "profit more quickly by their experience." But, he goes on to say, "if there be enemies still lower in the scale and incapable of forming such a mental association [between colour and inedibility] at all, then the destruction of butterflies which they would cause would have no effect whatever from a purely mimetic standpoint." It would be interesting to know whether Mr. Marshall is prepared to indicate the exact point in the descending scale of intelligence at which will occur the transition from the greatest efficiency in the production of Müllerian mimicry to no efficiency at all. Moreover, although the more intelligent enemy will doubtless learn its lesson more quickly, it may also, as Mr. Marshall points out in the next paragraph, discriminate more readily and therefore experiment more freely, the two tendencies acting to some extent in opposite directions.

With regard to Batesian mimicry, it does not seem altogether clear that superior intelligence operates quite as Mr. Marshall thinks it does. It may, on the one hand, as he says, enable the enemy to discriminate between mimic and model; but, on the other, it may also assist its possessor to recognise a warning sign which would be passed unnoticed by an enemy of lower mental equipment. It would not be easy to say for certain whether a close mimetic resemblance is an appeal to superior cleverness or superior stupidity. For such reasons as these I feel doubtful as to the validity of Mr. Marshall's expectation "that the elimination due to the Batesian factor would be competent to produce a higher degree of inter-resemblance than would the factor adduced by Fritz Müller."

In his next paragraph Mr. Marshall deals with a possible difference in the periods of incidence of the two mimetic processes. I am not sure that his account of the effect of the change of seasons can be taken as exact for all regions where the phenomena of mimicry obtain. For the country that has been the scene of his own admirable observations he can of course speak with the highest authority. But he appears to have left out of account the fact that it is not merely a question of young birds, but also of the emergence of new insects. The seasonal forms of butterflies are often so different from one another that a fresh brood may have to be learned as if it were a new species. Again, although in a given locality the insectivorous migrants may have departed, it is only to resume their activity among the insect provender, possibly quite new to them, of some other district. However this may be, the contention that the Müllerian factors vary in importance with the time of year, whether well-founded or not, does not seem to be very material for the points at issue.

We now come to an important section of Mr. Marshall's paper, in which on the strength of some very clever *a priori* reasoning, he asserts (I quote his words) that "a Müllerian approach will only take place in one direction, namely, from a rarer species towards a more abundant one, and no species can in this way approach another which has fewer individuals than itself." Equality (of number) he says, is "a condition which effectually prevents the Müllerian selection from producing any mimetic results" (p. 100). This contention rests principally on the arithmetical working out of certain supposed cases.

Before dealing specifically with Mr. Marshall's arithmetical demonstration, I would remark that experience shows the danger of trusting too much to *a priori* reasoning in matters of this kind, especially when its results do not accord with the facts of observation. In reference to an able treatise on a different subject,* lately published, it has been forcibly said that "readers are apt to assume that the statements are necessarily correct as being based on unimpeachable mathematical data. It will be well if they remember that mathematical deductions under the best conditions are like the flour that comes from a mill. If the original corn is impure, the flour will be unwholesome; . . . similarly arguments built up on insufficiently-observed phenomena, when subjected to the mill of mathematical reasoning, are exceedingly apt to have any faulty

* "Théories Modernes sur la Matière," by M. Pozzi-Escot.

observation magnified into grave and substantial error."* Or, as Huxley more tersely puts it, "mathematics will not give a true result when applied to erroneous data." As a single but sufficient instance, I would point to the history of a recent controversy.

Physicists, on what seemed to be very good *a priori* grounds, came to the conclusion that geologists and biologists had miscalculated the age of the earth. The biologists and geologists did not dispute the mathematical reasoning of the physicists, but they had confidence in their own facts, and they felt sure that there must be something wrong somewhere about the physicists' data. Their firmness has been justified; and the critics have now practically retired from the position that the geological clock wants altering.† Far be it from me to question Mr. Marshall's arithmetic. On arithmetical grounds which seem equally unassailable, it can be proved, as in the old logical puzzle, that if the tortoise once gets a start, Achilles will never catch him. What is the answer? *Solvitur ambulando.* We know that Achilles *will* catch the tortoise, arithmetic notwithstanding; and I venture to say that those who have fairly looked into the evidence know that Müllerian mimicry has taken place on a large scale, however difficult it may be to represent arithmetically the exact steps of its development.

Is there a flaw in Mr. Marshall's data? There are several flaws; as I shall show.

I shall begin by admitting that if in addition to his original assumption (pp. 97–98) we also allow him to suppose that the two hypothetical species are equally conspicuous, that they occur at exactly the same time, each form distributed at equal intervals throughout the same area, in which also their enemies are to be found with a similar evenness of distribution, and with a perpetually identical keenness of appetite, there is no doubt that the figures will work out nearly as he says; though even then it can be shown that there is a theoretical possibility of approach between two forms originally equal in numbers.‡

* "British Medical Journal," 1908, v. 1, p. 508.

† See Poulton, "Essays on Evolution," 1908: Essay on "The Age of the Earth."

‡ Because if the original number of each species, A and B, is x; the number of losses incurred by each species is y; and the number of A that assimilate themselves to B is n; the original chance of

But I venture to assert that this supposed case does not represent the usual, nor even a common condition of things in nature. This is no captious objection. I shall be able to show that Mr Marshall's supposed case, though interesting as an illustration of what might happen under certain conceivable circumstances, is valueless as a support of his position.

In the first place, he postulates, on the part of his two species of butterflies, A and B, the possession of "nauseous qualities in about the same degree." But every upholder of Müllerian mimicry, so far as I am aware, is not only ready to admit, but is prepared positively to assert that distastefulness is relative; that it exists, like other means of defence, in degrees that may vary indefinitely from species to species. Any one who doubts this needs only to refer to the experiments recorded by Mr. Finn in the "Journal of the Asiatic Society of Bengal," 1895 and 1897, to say nothing of Mr. Marshall's own results as published in the present and former papers (Trans. Ent. Soc. Lond., 1902, pp. 297–390; also *supra*, pp. 128–130). This cuts at the root of the statement that "a Müllerian approach will only take place . . . from a rarer species towards a more abundant one, and no species can in this way approach another which has fewer individuals (and therefore a higher percentage of loss) than itself" (p. 100). On the contrary, there is every reason to think that inferiority in numbers may be more than compensated by a higher degree of distastefulness.

The fact that different kinds of insect prey possess the qualities of palatability or the reverse in different degrees, and that these qualities are also relative to the likes and dislikes of different enemies, is fully accepted and enlarged upon by Mr. Marshall in a later section of his paper (pp. 128–130). But the strange thing is that he does not recognise that this conclusion, so far from being alien to F. Müller's theory, must form an integral part of any

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survival of each member of both A and B is $\frac{x-y}{x}$, but the chances of survival after the defection of n are—

For each member of A, $\frac{x-n-y}{x-n}$;

For each member of B (including the variety of A), $\frac{x+n-y}{x+n}$;

the advantage of B over A of course increasing with increasing values of n.

adequate account of the Müllerian conception. He has no warrant, so far as I am aware, for the statement that "in practice, the application of the Müllerian interpretation involves the assumption of a uniform standard of inedibility"; a statement which amounts to saying that any disparity of loss suffered by the less distasteful form involves the exclusion of the Müllerian factor from any assimilation it may acquire to the more distasteful. We can imagine that the frontier-line separating the operation of the two principles, though distinct, is fluctuating; but this does not justify any one in claiming the whole territory, up to the point of absolute equality of distastefulness, as an exclusive sphere of influence for the Batesian factor. In this and in other respects, Mr. Marshall's criticism, so far as it is effective, is directed not against the Müllerian theory itself, but against an imaginary position which has been erroneously endowed with the Müllerian name.

There is a further factor which has an equally disturbing effect with relative distastefulness on these numerical calculations. It is that of relative conspicuousness. A species poorly off in point of numbers may well suffer less than a more abundant form by dint of possessing a pattern which is more striking and so more easily remembered. A further complication is afforded by the varying habits of different species. It is by no means the case that all distasteful butterflies take every means of advertising themselves. There are differences between them in this as in other respects. As Mr. Marshall has mentioned the Erycinidæ * in this connection (p. 133), I commend to his notice the instructive case of *Hades noctula*, Westw., an abundant insect which there is every reason to suppose has acted as a model, but which nevertheless settles habitually on the under side of leaves.† If, as is quite possible, frequency of repetition is a factor in the rapidity with which insectivorous animals learn their lesson (a suggestion first made to me in a private letter by Mr. W. F. H. Blandford), a distasteful insect with habits of concealment might be more strongly influenced in the Müllerian direction than a species with great powers of advertisement though inferior in numbers. So far as

* Mr. Wallace's paper appeared in the Trans. Ent. Soc. Lond. for 1853; not 1863, as stated by Mr. Marshall.

† See Godman and Salvin; Biol. Centr. Amer., Rhopal., I, p. 374.

Mr. Marshall has dealt with this point at all, he has relegated it, like the former one, to the closing passages of his paper: and here again his argument suffers by reason of the exclusion from consideration, in its appropriate place, of what is really an important matter to be kept in view by all who would gain a clear and comprehensive grasp of the Müllerian hypothesis.

These then are the main reasons why Mr. Marshall's dictum about relative numbers cannot be accepted. Nor can we very well amend his arithmetical presentation of the case by restatement unless we assign numerical values, which can only be hypothetical, to the factors which he has omitted.

I think it will be seen that that part of the contention which depends merely on relative numbers must be withdrawn, and that my opponent must take his stand, if at all, upon the relative percentage of loss. A difference between species in this respect, by Mr. Marshall's own showing, will tend to the production of Müllerian mimicry; so that the only point on which I need join issue with him is his statement that "equality [in this case meaning an equal percentage of loss] effectively prevents the Müllerian selection from producing any mimetic results" (p. 100). The force of this contention is much weakened when we remember that there is no reason why the percentage of loss should remain constant while the individuals of a given form increase or diminish in number. In fact, from Mr. Marshall's own statement (p. 99) that "Müller's hypothesis postulates that the absolute destruction is practically constant for each group of different colours," it follows that the *percentage* loss must necessarily vary with every variation in the numbers of the group. Hence, as has been shown above (p. 563, note), Mr. Marshall's conclusion, even on his own data, is not quite correct. But there is still another factor to be taken into account which is sufficient to dispose of the objection altogether.

The supposed examples of distasteful butterflies, A and B, by hypothesis owe their survival to the possession of warning characters which are ultimately learnt by enemies and avoided when these latter have become sufficiently experienced. To employ Prof. Poulton's useful term, A and B are each of them provided with an aposeme; A's aposeme, also by hypothesis, being different from B's, and the two not being liable to be mistaken for one another.

Still keeping to the supposed case, and bearing in mind that A and B are each of them originally suffering the same percentage of loss, we find a certain number of A varying in the direction of B, that is to say, exhibiting an aposeme which is sufficiently like that of B to be confused with it. B and the variety of A, which we will follow Mr. Marshall in calling A′, now form, so far as B's aposeme is concerned, a homogeneous and mutually protective assemblage. But in adopting more or less of the aposeme of B, A′ has not necessarily lost hold of its original aposeme, and in every case where this is retained in recognisable form, A′ will share in the protection afforded by both aposemes, and will therefore have an advantage over both A and B, which by hypothesis are not mutually protective.

It will probably occur to any one who considers this point, that there must be a strong tendency towards the production and preservation of intermediate forms, stronger in the first instance than that towards the complete assimilation of one form to another. No doubt this is the case, and on examining actual instances we find plenty of indications of the operation of this principle. I shall have more to say on this head later on (see page 571), but it is incumbent on me, in the first place, to show how completely a recognition of the factor I am now discussing alters the whole aspect of reciprocal approach. I have implied already that I do not greatly favour the attempt to solve problems of this kind by means of numerical calculation; but Mr. Marshall has appealed to arithmetic, and to arithmetic he shall go.

We will suppose then, as Mr. Marshall does, two distasteful species, A and B, equal in numbers and distinct in appearance. We will also eliminate the effect of disturbing factors by supposing that the two species are equally distasteful, equally conspicuous and equally given to self-advertisement. Under these conditions the aposemes of A and B respectively will be learnt by the sacrifice of an equal number of A and of B; and as A and B are equal in population, this will mean that the percentage loss of each is the same. This is the state of things, reduced to its simplest expression, in which Mr. Marshall thinks that equilibrium will occur, and "the Müllerian principle will practically cease to operate altogether" (p. 99).

We will now express the case arithmetically. The actual numbers we take are immaterial, the only essential point being that they should be the same for A and for B. Let us say a population of 1000 for each. Now we will suppose that a certain number of A vary in the direction of B, so as to show the aposeme of B in addition to that of A; and that a certain number of B similarly vary in the direction of A so as to show the aposeme of A as well as their own, this of course being what is meant by a reciprocal approach. The possibility of the occurrence of such variations is allowed by Mr. Marshall (p. 98); what he does not allow is the possibility of their permanent establishment.

Again, numbers are immaterial; to keep the illustration as simple as possible we will suppose that the given variation of A amounts to half the number of the species, and that similarly B is equally divided between its original form and its variation. We now have four classes, each 500 strong, which we may call A, Ab, Ba, B; the small letters being used to signify the presence of an aposeme that is adopted and not original. Now we will suppose that 100 young insect-eating birds are let loose upon the butterflies of these four classes. To eliminate Mr. Marshall's complication of X, Y and Z birds (pp. 103–105) we will suppose that all the butterflies are exposed to simultaneous attack by the whole body of their enemies. It is obvious that on an average each class will be attacked by 25 birds. For the sake of simplicity we will further assume that the butterflies are so nauseous, or the palate of their enemies so delicate, that one experiment on each aposeme is sufficient to ensure the exemption of that aposeme from further attack by the experimenter. Now let us see what will be the fate of our four classes. The 25 birds that attack A will not touch it again. Neither will they experiment on Ab and Ba, which exhibit the same aposeme. But each of them will experiment on B, which has nothing about it to suggest A's aposeme. Hence the result of the attack of batch No. 1 is the destruction of 25 A and 25 B. Batch No. 2 experiments on Ab, destroying 25 of them. But it will attack none of the other three classes, because each of these possesses an aposeme which it has learnt to avoid. Similarly the 25 birds (batch No. 3) that take toll of Ba will henceforth avoid all the rest, for the same reason. Batch No. 4 devotes its attention to B, which has already suffered, or will suffer, under batch No. 1. Of this class B, 25 will be taken, without supplying any experience for the benefit of A, which latter class will therefore undergo a second exaction of the same number. The result of course is that the two original forms, A and B, each lose 50 individuals, or 10 per cent.; while the two diaposematic intermediates, Ab and Ba, each lose 25 only, or 5 per cent. Needless to say that in view of these considerations I have no intention of impaling myself on either horn of the dilemma so carefully prepared for me on p. 100 of my friend's paper.

It may possibly be objected that the numbers of Ab, Ba are not likely at the outset to be equal to those of A and B. This is true enough, but any one who is willing to incur the trouble can easily convince himself that taking the numbers of Ab, Ba smaller only accentuates their advantage over A, B. The number of individuals experimentally destroyed may of course be multiplied indefinitely without disturbing the relation between A, B and Ab, Ba.

But it may still be urged, is there any evidence that such intermediate forms as those exemplified in Ab, Ba are actually to be found in nature? Undoubtedly there is; about this I shall have more to say later on, but meanwhile we may take as a single example two forms of *Leuceronia* and *Nychitona* that occur together in the neighbourhood of the Victoria Nyanza. The former (*L. pharis*), though still unmistakably a *Leuceronia*, differs from its nearest allies by points in which it plainly approaches the *Nychitona*; while the latter, without losing its general resemblance to its own group, shows features of likeness to the *Leuceronia* which are peculiar to itself among its congeners. It may still be urged that there is no evidence of distastefulness in respect of these forms. This may be readily allowed without damaging the argument, for if such approach is possible between forms that belong to the edible category, it must be at least equally possible of occurrence between forms that are distasteful. And if it once occurs as a variation, its perpetuation is provided for in the manner already shown.

To summarise the foregoing:—Mr. Marshall has omitted to take into account the factors of (1) relative distastefulness, and (2) relative conspicuousness and powers of display. These omissions vitiate his argument as to the effect of relative population. Further, he has ignored (3) the effect of the possession of a double aposeme upon relative mortality, and (4) the fact that a persistence of a mimetic variation does not necessarily involve the disappearance of the type. These omissions destroy the remainder of the foundation on which his *a priori* fabric is based.

But perhaps, after all, it was unnecessary to offer one's own reasons for dissenting from Mr. Marshall's conclusions, for he has himself made two admissions which virtually undermine his case.

The first of these is that, as he puts it with great candour, "two lines of argument, based on the same data, have led to diametrically opposite results" (p. 101). This is a somewhat striking phenomenon, and ought of itself to suggest caution in dealing with these problems by numerical methods. In giving his view of the cause of the discrepancy, he fully recognises that his arithmetical argument is entirely competent to prove the advantage, to both sides, of any Müllerian combination *once effected*; though he holds that it does not succeed in accounting for the *process of formation* of such an assemblage, except in the case of considerable disparity of numbers. But when the process is complete, his difficulty ceases.

How is it then that he finds in the formation of a Müllerian assemblage a stumbling-block of this kind? The reason is that he is himself labouring under the error of which he accuses his opponents, viz., that in the representation of the case the intermediate stages are not adequately taken into account. The truth of the matter is that so soon as the aposeme of species B occurs in any of the individuals of species A, the Müllerian association B + A′ is already formed, and A′ enjoys its advantage. On Mr. Marshall's own showing, A′ now virtually belongs to B, which class is strengthened by its accession; and whatever may be A′'s chances of survival as compared with typical A, it has at any rate found a place in an assemblage which has so far been able to maintain itself. If its new character is of such a kind as to be subject to Mendelian laws of inheritance, there is no reason why it should not persist under the shelter of B, even in the absence of reinforcement from its original stock.

But a much more important consideration than the above is the fact that the first appearance of aposeme B is consistent with the persistence of aposeme A; a fact which is constantly overlooked, though it is really implicit in the statement that the Darwinian idea of the evolution of a case of mimicry (which is that accepted by Mr. Marshall) "involves the assumption that it has been built up by a gradual process of selection from comparatively small individual variations" (p. 101). The intermediate form with its double aposeme at once brings the Müllerian factor to bear throughout the whole assemblage which it unites. It is not always realised how easily the gap between A and B may be bridged over. Take the case of *Pieris demophile* (both sexes) and *Acria agna*, a Pierine and an Ithomiine from Brazil. All that is necessary is to insert the yellow form of *P. demophile* ♀ between the normal types of the two species, and the chain is complete from end to end; moreover, it becomes linked on to the great assemblage of which *A. agna* is a representative. I do not assert that this particular association is Müllerian; I only adduce it to show how easily a Müllerian couple might be established. It illustrates some other points as well, viz. (1) that the rise of a mimetic variation does not necessarily involve the extinction of the parent form (this survives in typical *P. demophile*), and (2) that distasteful intermediates may be conceived of as mutually protecting and being protected by the distasteful forms not on one side only, but on each side of them. This last point is of course only another way of putting what I have already spoken of as the function of the double aposeme. It is obviously of the first importance for the right understanding of Müllerian mimicry.

It may be said, in reference to the foregoing, that I have taken a case where mimic and model are already somewhat alike. Let me therefore now show how the two hypothetical species A and B may be brought into association with one another, though originally very dissimilar in aspect. If we were to confine ourselves to theory, I admit that the process might be somewhat difficult of conception. But when we turn to the actual facts of such a case, we see how the passage may be helped along by the existence of other species, each of which is capable of forming a collateral association with the transitional forms in turn. Thus, a very slight modification of the yellow form of *P. demophile* ♀ gives us another Pierine form, that of *P. viardi* ♀, which aligns itself with *Heliconius charithonia*; while a short step onwards from *P. viardi* brings us to the form now called *P. tithoreides* ♀, the mimetic relation of which with *Tithorea pavonii*, *H. atthis*, and the *peruviana* form of *H. charithonia* will only be questioned by those who do not accept the doctrine of mimicry at all.

There is no need to multiply instances, though it could readily be done. The point required is to recognise the fact that a mimetic chain can be built up by successive small steps, each of which secures at once the condition which Mr. Marshall himself maintains is favourable to the Müllerian relation; for he allows, as we have seen, that when the association is once formed, the advantage to all parties, whatever the relative numbers, can be demonstrated by arithmetic.

This first concession, when followed out into its consequences, appears to me of itself sufficient to dispose of the only serious objection brought on *a priori* grounds against the possibility of Müllerian approach, whether from one side or from both, even in those cases where both species may be equally "dominant." But if this were not so, Mr. Marshall's second concession (p. 103) would really give me all I want, for by it he asserts the possibility of the very interchange that I have all along been holding in view. I am not disposed to raise a controversy about the mere use of words, and if Mr. Marshall prefers his own term "Alternate Mimicry," I have no objection to offer; the point is that he allows the same possibility that I maintain; the occurrence, that is, of a give-and-take process between so-called "mimic" and "model." This is the essence of what has been called Reciprocal Mimicry or Diaposematism, for which terms I could suggest no more suitable definition than "the interchange of characters between distasteful forms in virtue of their distastefulness." No one could suppose that every step from the one side is exactly in point of time coincident with a step from the other; nature works on successive individuals, and whether or not at any given moment the general trend is in one direction rather than another is immaterial. Moreover, it is conceivable, even on Mr. Marshall's principle, that the tendency might take opposite directions at the same time in different parts of the area of distribution.

Particular Instances of Diaposematism.

So much for the attempts that have been made to impose limitations *a priori* on the scope of Müllerian mimicry, and in especial to disallow the possibility of that interchange of features between distasteful forms which is known as Diaposematism or Reciprocal Mimicry. I now turn to the particular criticisms which Mr. Marshall makes on the diaposematic interpretation of certain concrete and definite instances.

With regard to these instances, I would in the first place observe that they are not all of equal strength, and that, as I have always been ready to admit, there is perhaps not one of them that is absolutely incapable of being explained on other lines. But their force, as it seems to me, lies in their cumulative effect. Let me give an illustration. Suppose that on a riding or driving tour through the country, you see, on approaching a town, a boy wearing a straw hat with a variegated ribbon. By and by you meet with another boy, then with two or three more, finally perhaps with a little crowd of boys, all with the same coloured hat-ribbon. The first occurrence makes no special impression on you, nor perhaps the second or third, but before long you awake to the fact that there must be some common cause for this constantly recurring phenomenon, which cause will probably declare itself as the existence of a school or an athletic club. So with these instances of apparent interchange. Taken separately, each one may be put down to accident, coincidence, affinity, or what you will; but as cases begin to accumulate, any explanation short of the influence of some common law or principle ceases to be satisfactory. With respect to Mr. Marshall's remark that no example of Diaposematism has as yet been brought forward as occurring between any two of certain groups that he specifies, it may be sufficient to observe that these groups, so far as I am aware, have never yet been studied from this particular point of view.*

The Association of Pereute *and* Heliconius.

Under this head I am pleased to find that Mr. Marshall at least agrees with me that there is a mimetic relation between the *melpomene* group of *Heliconius* and a *Pereute*, though Mr. Kaye would perhaps differ from us both (see his communication in Proc. Ent. Soc. Lond., 1908, pp. xxii, xxiii). But Mr. Marshall, in commenting on my suggestion that the *Heliconii* which enter into mimetic combination with Pierines have been influenced by the latter "in adopting from them a more distinct and characteristic employment of the red basal patches," remarks that "in order

* See however Fritz Müller (translation by Meldola in Proc. Ent. Soc. Lond., 1879, p. xxviii), who actually alleges cases, though without giving details.

that any case of this kind may really carry conviction as a proof of diaposematism it is necessary to show that the reciprocal character which the model is claimed to have acquired from the mimic must be one that is abnormal in the genus of the model and its allies." On this I would observe that if Mr. Marshall will look again at my paper from which he quotes (Trans. Ent. Soc. Lond., 1894, pp. 296–298), he will see that I do not claim that the existence of the red basal patches in *Heliconius* has been "acquired from the mimic." On the contrary, I am in that passage at pains to show that there already exists in *Heliconius* material in the shape of red basal markings for the aposeme that becomes especially conspicuous in those species which enter into mimetic relation with red-spotted Pierines. Hence his enumeration of red-spotted *Heliconii* is beside the mark, for he has not met my assertion that the spots are especially distinct and characteristic in these mimetic species. My view was and is that the Pierines have contributed to the special appearance presented by the spots in certain species; not that they are actually responsible for the origin of those marks. I fear I cannot agree that a character such as this, if reciprocally adopted, must be "abnormal in the genus of the model and its allies," for in most cases there will be found already existing, as might be expected, some basis for the assimilative process to work on.

While the *Heliconii* are under consideration, it may not be amiss to remark on the great plasticity exhibited by this genus, so far as concerns its colour-patterns. This is exemplified by the large number of species which, as Mr. Marshall says, "have been drawn away in mimicry of the great *Melinæa-Mechanitis* association," and still more by the completeness with which members of one of the two great groups into which the genus falls have become assimilated in aspect to species belonging to the other.* Mr. Marshall himself suggests that the absence of red spots in the *Melinæa*-like *Heliconii* may be due to mimicry, which shows that in his view this feature of the Heliconine pattern is not resistent to mimetic influence. As regards the Pierines, there is no reasonable doubt that the red basal aposeme in *Delias* has impressed itself not only upon *Prioneris* but also on Chalcosid moths (see Shelford, Proc.

* See Riffarth and Stichel, in the "Thierreich," 1905; also W. J. Kaye, Proc. Ent. Soc. Lond., 1907, pp. xiv–xvi.

Zool. Soc. Lond., 1902, vol. ii, No. 257, Plate XXI, figs. 1–4). There is, therefore, no antecedent improbability in the supposition that the corresponding aposeme in the South American Pierines under discussion, less marked but still conspicuous, should have been able to exercise an influence upon the *Heliconii*.

In Mr. Marshall's review of the genus *Pereute* (p. 108) I find myself quite unable to follow him. I confess that I do not understand his statement that it is only in his third section "that we find any real mimicry." I should have thought that mimicry if it exists at all must be real. If he only means that some species are closer mimics than others, of course I agree with him, but the remark in this connection hardly seems worth making. As to the main point, I do not think that any one who undertakes a thorough examination of the genus in relation with other butterflies of the Neotropical region can avoid coming to the conclusion that every species of *Pereute*, even including *P. telthusa*, displays mimetic features. Mr. Marshall's South African experience will suggest to him that to make the examination complete, the under-sides must be included in the study; as indeed in one place he seems to imply.

The under-side red spots in Archonias (*or* Euterpe) tereas *and* Papilio zacynthus.

Under this heading Mr. Marshall has—I am sure unintentionally—given so complete a misrepresentation of my published statements, that I can only suppose him to have omitted to make himself fully acquainted with them. It would, I think, be inferred by any reader of his criticism that I had advanced the view that the *Papilios* belonging to the colour-group of which *P. zacynthus* may be taken as an example had adopted their under-side red spots in mimicry of the associated Pierines (pp. 109, 110). How far such a supposition is removed from my real opinion will be made sufficiently clear by an extract from the very paper that Mr. Marshall quotes as his authority, viz. my memoir on the Pierinæ published in our Transactions for 1894. In a note on page 285 of that memoir occurs the following passage dealing with the butterflies in question:—"The red basal patches on the under-side of the Pierine give just the same general effect as similar patches on the *Papilio*; but a close scrutiny will reveal the curious fact that the patches of the Pierine belong always to the wing, and those of the *Papilio*, in almost every instance, to the body. The wide distribution of the red basal patches among the *Pierinæ* forbids us to suppose that they were evolved for the purpose of mimicry in these few species; but it is worth noting that their presence affords material ready to hand for a sufficiently deceptive though not absolutely exact copy of a conspicuous Papilionine feature."

It will be seen from the above quotation that the position of the red spots on *Papilio* and Pierine respectively had already been noted and taken into account by me, though this would not be gathered from Mr. Marshall's description on pp. 109, 110. It is also plain that although (like Mr. Marshall) I could not regard the red spots as having come into existence in the Pierine for the sake of mimicking the *Papilio*, I was prepared to entertain the view that so far as position and general appearance were concerned they had undergone Papilionine influence. The fact that many *Papilios*, both mimetic and non-mimetic, are red-spotted, was of course well known to me, and is duly stated in the same paper (Trans. Ent. Soc. Lond., 1894, pp. 296, 298). In these latter passages I suggest the possibility, which still appears to me quite reasonable, that *Papilios*, *Heliconii* and Pierines, all possessing suitable material for working upon, have each, in the case of these mutually mimetic species, contributed something towards the general agreement. The main points in favour of an exercise of Pierine influence, I may repeat, are (1) the prevalence of the basal red throughout the subfamily; (2) the fact that the genera *Euterpe* and *Pereute* are probably closely allied to the distasteful Eastern genus *Delias*; and (3) the fact that some species at any rate of *Euterpe* and *Pereute* are reported by field naturalists to be abundant in individuals. The suggestion that these South American Pierine "mimics" might themselves act in some respects as models was in 1894 so new, and so contrary to received ideas, that I dwelt on the evidence in question with some emphasis. I still think the evidence strong. So far as Mr. Marshall pronounces in favour of an independent origin of red spots in all these three subfamilies, I agree with him; my expressed view has always been the same. If however he really means that no mimetic modification of the spots has taken place as between these groups, I think that those naturalists who are well acquainted with the species concerned will regard his conclusion as a *reductio ad absurdum*.

Why do both sexes of Archonias (Euterpe) tereas *mimic only the females of* Papilio zacynthus ?

In this section of his paper Mr. Marshall makes the curious statement that "not a single one of the American Pierines has developed any metallic colours" (p. 111). By "metallic colours" he shows in the same passage that he means an iridescence or glow such as may be seen in certain African species of *Teracolus*, for example in *T. regina*, where it exists in a highly-developed condition. Has Mr. Marshall ever looked at *Dismorphia teresa* ? Or at the male of *Meganostoma eurydice*, or of *Colias lesbia* and *C. vautieri* ? Or at a fine male specimen of *Phœbis argante* ? Even in the Pierine genus at present in question, it is by no means rare for a well-preserved example of *Euterpe approximata* or *E. critias* to exhibit a purple gloss on the hind-wing, a gloss which, though comparatively undeveloped, recalls that of many *Papilios*. The fore-wings of *E. antodyca* ♀ and *E. swainsonii* ♀ often show a similar bloom. Then as to African forms, has Mr. Marshall forgotten *Colias electra*, of which he must have seen innumerable specimens ? There can I think be no doubt that there is nothing in the Pierine constitution to prevent the development of "metallic" colouring, should the opportunity and need for such development arise in the history of a species. In reference to F. Müller's statement that although in his experience *Euterpe tereas* was common, and *Papilio nephalion* rare, the latter must be regarded as the model rather than the former, Mr. Marshall seems to be quite alive to the fact that if this case of mimicry is, as he says, "in every way consistent with the interpretation of a simple Müllerian approach," it remains an instance that *primâ facie* requires a good deal of reconciling with his view as to the improbability of Müllerian approach even when the numbers are equal, and much more when the numbers of the "model" are inferior. I myself should of course agree with F. Müller that the Pierine has adopted most of its peculiar aspect in imitation of the *Papilio*; but I should not consider that this precludes the female *Papilio* from having been retained by the help of Pierine influence within the limits of the strong combination thus formed. Mr. Marshall's opinion that the female pattern is the older is very likely to be correct; it has always seemed to me the more probable supposition; though, in view of what may be seen in many other groups, I should not venture to exclude altogether the possibility that the female may have dropped some characters once common to both sexes and even gained others under the influence of mimicry or some other form of adaptation. This is why I suggested in 1894 that the female *Papilios* had joined the *Euterpe* combination whether by "discarding" or [supposing the females to represent the older form] by "not adopting" the brilliant colours of the other sex (Trans. Ent. Soc. Lond., 1894, p. 298). It was pointed out by me many years ago (Trans. Ent. Soc. Lond., 1890, p. 106, note, *à propos* of *Argynnis diana* ♀; and again in Proc. Ent. Soc. Lond., 1894, p. xii, *à propos* of *A. niphe* ♀) that a mimetic resemblance may be attained by the help of the retention of an ancestral character no less than by the development of a new one. Mr. Marshall's point would only tell against my suggestion if this possibility were ignored.

The suggested reciprocal resemblance between Pieris locusta *and* Heliconius cydno galanthus.

Mr. Marshall begins his discussion of this case as follows:—"In Trans. Ent. Soc., 1896, p. 72 (note), Dr. Dixey suggested tentatively that *P. locusta* ♂ was a mimic of *Heliconius melpomene,* so far as the underside of the hindwing was concerned. In Trans. Ent. Soc., 1897, p. 325, this idea was abandoned, and the very different *H. cydno galanthus* was then definitely proposed as the model" (p. 113). I shall hope for Mr. Marshall's forbearance if I venture to point out that this is scarcely an accurate way of putting it. My words in 1896 were, "The underside of the hindwing in *P. locusta*, *P. cinerea* [I should now write *Leptophobia cinerea*] *and some others* resembles that of *Heliconius melpomene and other protected species* in giving the general idea of a dark wing-area with yellow costal or precostal streak and basal red spots." I have never "abandoned this idea," which indeed is merely the expression of a simple matter of fact; but in 1897 I gave the general statement above quoted a more special application by instituting a comparison between the under side of *P. locusta* ♂ and the *cydno* group of *Heliconius*; even then being careful to point out that "the aspect suggested [by *P. locusta* ♂ underside] is rather that of several forms of *Heliconius* in general than that of any one in particular." Why Mr. Marshall should think it necessary to show that the upperside of *P. locusta* ♂ is non-mimetic "and can have no significance during flight" (p. 113) I am at a loss to understand, for I myself expressly stated that "it is only on the underside that the mimetic pattern appears, and here again there can be little doubt that its use has reference only to the resting position." Mr. Marshall appears to disbelieve that any mimetic significance whatever attaches to either surface of the male *P. locusta*. In this opinion I think few impartial observers will follow him.

With regard however to the "fair general resemblance" which he admits to exist between the upperside * of the female of *P. locusta* and the *galanthus* form of *H. cydno*, he arrives at the conclusion "that the most satisfactory interpretation of the present case is that the ♀ *Pieris* is a simple Batesian mimic of the *Heliconius*." In support of this position he makes some remarkable statements. "It is only fair to point out," he says, "that when this proposal" [i.e. my suggestion as to the association of *P. locusta* with the *cydno* group] "was made, the true ♀ of *P. locusta* was not known, the ♀ figured by Dr. Dixey belonging really to *P. tithoreides*, Butl." I regret to have to correct Mr. Marshall on a point of fact, but he will find on further enquiry that the female of *P. locusta* was then known and had been described by Felder. I figured the local race (or geographical species) *tithoreides* under the designation of the type form, for the simple reason that there was then no other name by which to call it, its present title not having been bestowed upon it until some time later.† I do not know on what grounds Mr. Marshall pronounces *P. locusta* ♀ to be "evidently a rare insect." Felder's account ‡ implies that the species is common. I can of course readily believe that the male falls a more easy prey to collectors.

* Why not also the underside? Can it be because this would carry a similar conclusion in the case of the male?

† *P. tithoreides* was first described by Butler, Ann. Mag. Nat. Hist., 1898, ii, p. 18.

‡ Reise d. Novara; Rhop., p. 176.

In stating that "the crux of the whole argument lies in the assumption that white colouring is abnormal in *Heliconius* and must therefore be due to Pierine influence" (p. 114), Mr. Marshall is labouring under a similar misapprehension to that which led him to attribute to me the view that the existence of red spots in *Papilio* originated in mimicry of the Pierines. I have shown that my expressed view was the contrary of this, and that I regarded and still regard the original red spots in both groups as affording material for an assimilative process of which there remain in existence many traces. In exactly the same way I look upon the occasional presence of white patches and bands in *Heliconius* as the raw material from which a resemblance to the broad white areas of the usual Pierine aspect has been in certain species manufactured. Any one who has not realised how much like a Pierine a *Heliconius* can be made to look, should compare the *leuce* form of *H. sapho* with the female of the form of *P. locusta* known as *noctipennis*.

The suggested diaposematic resemblance between the two Eastern Pierines Huphina corva *and* Ixias baliensis ♀.

It would, I think, hardly be inferred from Mr. Marshall's account of this example that nearly all the points which he raises had already been taken into account by me and allowed due weight in my paper which he quotes. Thus the difference between the under sides of the *Huphina* and the *Ixias* is in that paper both mentioned and specially figured, while an explanation is offered which is probably valid in several similar cases (Trans. Ent. Soc. Lond., 1906, p. 522). The fact that the dark border of the hind-wing is better defined in the male than in the female *Huphina* is of course perfectly apparent in my figures (*Ibid.*, Pl. XXXI). These show that although in this particular respect the male has the advantage, the female is still on the whole the better mimic. They also show that the "heavy black bar across the cell of the fore-wing" is not "entirely absent" from the male, as Mr. Marshall alleges, but present in the corresponding position to that which it takes in the female, though of course in the former sex it has not reached so high a stage of development.

The facts as to the geographical distribution of the two species were carefully noted by me (*loc. cit.*, p. 523), as indeed Mr. Marshall acknowledges. He very truly points out that "if we examine such a series of forms as *Huphina phryne*, *nerissa*, *lichenosa* and *corva*, it seems clear that we are dealing with those progressive modifications which are generally comprised under the name of geographical races." It is also quite correct that "heavy black borders are a very common feature in the genus *Huphina* and exist in a majority of species occurring in the Malay Archipelago." Then why should we assume that the line "leads up" from *H. nerissa* through *lichenosa* to *corva*? Is it not equally open to us to suppose that *corva* began in the Malayan region where so many of its congeners find a home, and passed towards the north and west, gradually losing its black border as it came into new geographical surroundings, but retaining that feature so long as it was subject to the mimetic influence of *Ixias*? If this supposition be rejected, there remains the possibility, or even probability, of other distributional changes. These are more important factors in mimicry than has, I think, been generally admitted.* But the elevation of the present facts of distribution, interesting as they are, into a "serious difficulty" in the way of the diaposematic interpretation of this very curious resemblance seems to savour of hypercriticism; as also, especially in view of Mr. Finn's experiments referred to in my paper,† does Mr. Marshall's evident scepticism even as to the mimicry of *Huphina* by *Ixias*. As to Mr. Wallace's "warning" quoted by Mr. Marshall (pp. 120, 121), I am not in much danger of forgetting it, for I know now that I have several times in the past been temporarily misled into attributing to fortuitous resemblance or to mere affinity many undoubted cases of Pierine mimicry.

The fact mentioned by Mr. Marshall that the British Museum specimen of *I. baliensis* ♀ possesses a suffusion of pale orange in the central area of the fore-wing, a point which had also been noted in my paper (*loc. cit.*, p. 523), is especially interesting; as it shows that in this species the mimetic process is not entirely complete.

The last point which seems to call for remark in this

* See Poulton, "Essays on Evolution," 1908, p. 52; and note by Mr. Trimen on recent changes of distribution in African butterflies, *ib. cit.*

† The reference was given by me as "Journ. Asiat. Soc. Bengal," 1895. The year should be 1897.

connection is the difference in character of flight shown by the two genera concerned. It is of course no proof of palatability or the reverse that an insect is active and wary on the wing. Many distasteful species, especially the "dominant" models, possess the characteristically deliberate demeanour first noticed by Bates, but others show resemblances of greater or less degree in this, as in other respects, to the forms that usually occupy central positions in mimetic groups.

Here ends my survey of Mr. Marshall's criticism of particular instances. I feel justified in maintaining, as a result of this examination, that not only has he failed in each single case to prove his point, but that he has also in many particulars been betrayed into actual error.

The remaining examples impugned by Mr. Marshall, together with that portion of the concluding section of his paper which has not been dealt with by me, bear reference to certain views and observations for which I am not personally responsible. I shall not presume to enter the lists in defence of champions so well able to take care of themselves as my friends Prof. Poulton and Mr. Neave; but it may not be out of place to add here a remark with regard to Mr. Marshall's footnote on page 122 of his paper. He there calls attention to some apparent discrepancies in the accounts given by Dr. Longstaff and myself of the scents of certain African butterflies. It is a well-established fact that scents of opposite character may coexist in the same individual (instances are given in my communication quoted by Mr. Marshall from Proc. Ent. Soc. Lond., 1906, pp. ii–vii), and it seems probable that the differences between Dr. Longstaff's records and my own—a very few differences, be it noted, amidst a large body of substantial agreement—may be attributed to a reason of this kind. Certainly my recollection of the strong, disagreeable odour of *Neptis agatha* is vivid to this day.

Before concluding this paper I have a suggestion to offer to students of the Müllerian problem who may still be in an early stage of their investigations. It is that those who wish to avoid a cramped and narrow view of the mimetic problem should refrain from stating and considering it only in terms of "mimetic pairs" or even "mimetic associations." The real unit of study is the aposeme, in its transitions, its modifications and its combinations. This will lead, amongst other things, to a recognition of the important principle of "secondary mimicry"; a powerful reinforcement of the Müllerian interpretation, which has been omitted from consideration by Mr. Marshall, and on which accordingly I do not enlarge. A final point to be impressed upon those who may be approaching the question for the first time, is the wonderful insight into future developments of his theory shown by Fritz Müller himself. Reference to Prof. Meldola's translation of Müller's truly epoch-making paper in Proc. Ent. Soc. Lond., 1879, pp. xx–xxviii, will show that not only is the main principle most clearly and precisely there stated, but that the author also foreshadows such subsidiary points as relative distastefulness, "alternate mimicry," the unpalatability of Pierine "mimics," and not only the possibility but even the actual existence of diaposematism.

The kind expressions used by Mr. Marshall on the last page of his paper I should wish most cordially to reciprocate. I may go further, for I believe that I owe more benefit to the results of his experience as a field naturalist and skill as an experimenter than he can have derived from any publications of mine. I am not at all fond of controversy in itself, though I admit its value and occasional necessity. But if one has the misfortune to differ from a friend and fellow-worker in the same field, the regret that is unavoidably felt is much mitigated when one meets so courteous and fair-minded an opponent as on the present occasion.

However, Mr. Marshall has now shot his bolt. It has failed; and the upholders of the large and comprehensive principle of Müllerian mimicry, including its corollary of Diaposematism or reciprocal influence, may await with equanimity the delivery of attack from any other quarter.