Mr. Wallace on Physiological Selection

IN the September issue of the *Fortnightly Review*, Mr. A. R. Wallace published an article criticising the theory of physiological selection, and subsequently published a letter in NATURE conveying the substance of that criticism. Having now replied to all my critics in the current issue of the *Nineteenth Century*, I will here give the substance of my answer to Mr. Wallace.

"(1) Mr. Romanes makes a great deal of the alleged 'inutility of specific characters,' and founds upon it his extraordinary statement that, during his whole life, Darwin was mistaken in supposing his theory to be 'a theory of the origin of species,' and that all Darwinians who have believed it to be so have blindly fallen into the same error. I allege, on the contrary, that there is no proof worthy of the name that specific characters are usually useless, and I adduce a considerable series of facts tending to prove their general utility."

Now, in this matter I not only "allege," but prove, that I have upon my side Darwin himself ("Origin of Species," pp. 171, 176, 421; "Descent of Man," p. 61) and more or less "all Darwinians." Moreover, I have shown that the arguments whereby Mr. Wallace seeks to justify his own individual views are quite unworthy of their distinguished author.

"(2) In support of his view as to the swamping effects of intercrossing, Mr. Romanes objects to the assumption of Darwin, 'that the same variation occurs simultaneously in a number of individuals,' adding: 'Of course, if this assumption were granted, there would be an end of the present difficulty'; and his whole argument on this branch of the question rests on the assumption being false. I adduce evidence—copious evidence—that the supposed assumption represents a fact, which is now one of the best-established facts of natural history."

The "copious evidence" here alluded to consists merely in a reference to the well-known observations of Mr. J. A. Allen upon the kinds and degrees of individual variation exhibited by certain species of American birds. I am able to show that none of these observations have any bearing upon the "difficulty" in question; and that so far from the "assumption" in question representing "a fact which is now one of the best-established facts of natural history," even so accomplished an ornithologist as Mr. Seebohm displays so sublime an ignorance of its establishment as to affirm, in his criticism of my paper, that "it is seldom that the difficulties of natural selection from fortuitous variations have been so clearly, so impartially, but so candidly set forth." And he adds, *speaking specially of birds*, "So far as is known, no species has ever been differentiated without the aid of geographical isolation," *i.e.* without some check upon free intercrossing.

"(3) Mr. Romanes states, as the special feature of his physiological varieties, that 'they cannot escape the preserving agency of physiological selection.' He gives no particle of proof of this, while I show that, on the contrary, it is hardly possible for them to survive to a second or third generation."

The objection here is that the chances must be greatly against the "physiological complements" (or the suitably varied individuals of opposite sexes) happening to mate, and, even if they did, that their progeny should likewise do so often enough to start a permanent variety.

In answer to this objection I first of all adopt my critic's assumption, namely, that in all cases physiological selection must depend on the chance unions of physiological complements, relatively very few in number, and scattered over areas occupied by large species. Upon this assumption I agree that the sexual variation, "whenever it occurs, is almost certain to die out immediately," after which the paper proceeds as follows:—

"Granting it is shown that the union of these physiological varieties of opposite sexes is a matter of enormously rare occurrence, is it not also true that *the origin of a new species is an enormously rare event?* Not a few existing species have remained unchanged from remote geological time; the life of all species is incalculably long as compared with that of their constituent individuals; and in every generation of individuals there are, in the case of most species, millions of fertile unions. Therefore, so far as we can form any estimate on a subject where all proportion seems to fail, we may safely conclude that the ratio between the number of species which have appeared upon this earth, and the number of fertile unions between their constituent individuals, can only be represented by unity to *billions*.

"In view of this fact I am not afraid of any calculation that can be made, in order to show how many chances there are against the confluence of those conditions on the occurrence of which my theory supposes the origin of a species to depend. According to Mr. Wallace's estimate, the chances against the suitable mating of these physiological varieties 'may be any number of *thousands* to one'; so that, in view of the considerations above given, and the large number of species existing at any one time, we might conclude that Mr. Wallace supposes the birth of a new species to be an event of almost daily occurrence. Therefore, looking to what we all know are the real facts of the case, even if it were true that whenever one of these physiological varieties occurs, 'it is almost certain to die out,' this *almost* may be here quite sufficient for all that is required. Thus, upon the whole, and under my temporary acceptance of Mr. Wallace's assumptions, I confess it appears to me a somewhat feeble criticism to represent that the conditions which my theory requires for the origin of a new species are probably about as rare in their occurrence as is the result which they are supposed to produce.

"So much, then, for my first answer. My second answer simply is that from its beginning to its end this criticism is wholly in the air. Hitherto I have been considering his assumptions merely for the sake of argument. But they are not *my* assumptions; they form no part of my theory; and, therefore, I repudiate them *in toto*. The paper which Mr. Wallace is criticising clearly and repeatedly sets forth that I do *not* suppose the mating of physiological varieties to be wholly a matter of chance. Whether or not it is a matter of chance will depend on the causes which determine the variation. When these causes are of a kind which act simultaneously on many, on most, or even on all individuals occupying the same area, the element of chance is proportionally excluded. One very obvious, and probably frequent, instance of what may be termed collective variation in the reproductive system—or a variation due to a common cause acting on many individuals simultaneously—is actually quoted from my paper by Mr. Wallace himself, namely, changes in the season of flowering or of pairing, which insure that any section of a species so affected shall be fertile only within itself. Collective variation of this kind may be directly due to the incidence of some common cause, such as changed conditions of life with respect to food, climate, station, &c.; or, as in the case of bud-variation, it may be due to a single 'sport' affecting all the blossoms growing *upon the same branch*. But besides such *direct* action of a common cause, it is easy to see that natural selection, use and disuse, &c., by operating in the production of organic changes elsewhere, may not unfrequently react on the sexual system *indirectly*, and so induce the sexual change required in a number of individuals simultaneously. All the parts of an organism are so intimately tied together, and the reproductive system in particular is known to be so extraordinarily sensitive to slight changes in the conditions of life, or to slight disturbances of the organic system generally, that in their work of adapting organisms to changes of their environment all causes of an 'equilibrating' kind must be calculated more or less frequently to affect the reproductive system in the way required. . . .

"If I have succeeded in making myself intelligible, it will have been seen that Mr. Wallace's objection to my theory admits of a twofold answer. In the first place, it is impossible for him to 'show' that the origin of a species is any more frequent than it ought to be, even upon the assumption which he has imputed to me—namely, that such origin is always due to the chance mating of more or less extremely rare varieties. And, in the next place, this assumption on his part is wholly gratuitous—or rather, I should say, directly opposed both to my own statements and to all the probabilities of the case.

"From which it is easy to perceive the inevitable inference, or, if not, by stating it I will furnish a cue to future critics. *The real difficulty against my theory is precisely the opposite of that which Mr. Wallace has advanced.* This real difficulty is that the differentiation of specific types has not been of nearly so frequent occurrence as upon the theory of physiological selection we should have antecedently expected. Looking to the great sensitiveness of the reproductive system, to the many and the varied causes which affect it, to the frequency with which these causes must have been encountered under Nature, to the fact that whenever a collective variation occurs of the kind which induces physiological selection it must almost certainly leave a new species to record the fact—looking to all these things, the only real difficulty is to explain why, if physiological selection has ever acted at all, it should only have done so at such comparatively rare intervals, and therefore have produced such a comparatively small measure of result. If my critics had adopted this line of argument I should have experienced more difficulty in meeting them. But, as the case now stands, it seems enough to remark that I do not know of any way in which an adverse criticism admits of being more thoroughly exploded, than by showing that the difficulty which it undertakes to present is the precise opposite of the one with which an author is in his own mind, and at that very time, contending.

"Seeing how remarkable has been the misunderstanding displayed by such competent readers as Mr. Wallace and Mr. Seebohm—a misunderstanding on which they both found their only objection to my theory—I should have been compelled to suppose that my paper failed in clearness of expression, were it not that (as above shown) they have disregarded the literal construction of my sentences. Nevertheless, it is probable enough that I may not have sufficiently guarded against a misunderstanding which it never occurred to me that any one was likely to make. For I supposed that all readers would have perceived at least that the main feature of the theory is what my paper states it to be—namely, that sterility with parent forms is one of the *conditions*, and not always one of the *results*, of specific differentiation. But, if so, is it not evident that all causes which induce sterility with parent forms are comprised by the theory, whether these causes happen to affect a few individuals sporadically, a number of individuals simultaneously, or even the majority of an entire species?"

GEORGE J. ROMANES

Mr. Wallace on Physiological Selection

SEEING that Mr. Wallace has now changed front with regard to some of the points at issue between us, I must once again address you upon this subject.

(1) He appears to have forgotten that the whole plan of his original impeachment consisted in representing me as an arrogant heretic. This impeachment was published under the heading "Romanes *versus* Darwin," and point by point it laboured to show that I was deserving of excommunication as a rebel against the highest authority. In my reply, therefore, I was obliged to show that the charge was misdirected; and this I did by simply quoting passages from that highest authority himself. It is needless to say that I am now as much satisfied as surprised to find this charge, not only abandoned, but reversed. Whereas I was previously accused of presumption for disregarding authority, now the remonstrance is—"he appeals to authority against me," and "I decline to accept authority as an infallible guide." So do I. But I quoted my authority merely for the avowed purpose of defending myself from the specific charge of my opponent. It was *he* who appealed to Cæsar, and cannot therefore now complain if to Cæsar he had to go. Truly, if I may employ his own mode of expression, "further discussion of the matter with such an adversary is out of the question."

(2) But, as regards one of the points, he says that my quotations appear to him to support his own views rather than mine. The shortest way of testing the value of this judgment will be to print in succession three passages, which I have selected as serving in each case most concisely and most fairly to embody the opinion of its writer. The point in question is as to whether specific characters are "invariably" adaptive, or "frequently" not so, and the italics are mine.

"When, *from the nature of the organism and of the conditions*, modifications have been induced which are *unimportant* for the welfare of the species, they *may be*, and *apparently often have been*, transmitted in nearly the same state to numerous, otherwise modified, descendants." (Darwin, "Origin of Species," p. 175.)[1]

"I believe, therefore, that the *alleged* inutility of [many] specific characters claimed by Mr. Romanes as one of the foundations of his new theory, *has no other foundation* than our extreme ignorance." (Wallace, *Fortnightly Review*.)

"The matured judgment of Mr. Darwin clearly recognised the distinction between the origin of *species* and the origin of *adaptations*, —a distinction, indeed, which necessarily follows from his repudiation of the doctrine of utility as universal. . . . . Therefore, with him I believe that an incalculable number of specific characters are of an adaptive kind, and that many more which now appear to us (in our ignorance) to be useless, will hereafter be proved to be useful. But with him also I believe that *a large proportional number* of such characters actually are destitute of utility, having been due, as he says, to 'fluctuating variations, which sooner or later became constant through the nature of the organism and of surrounding conditions, as well as through the intercrossing of distinct individuals; *but not through natural selection*.'" (Myself, *Nineteenth Century*.)

(3) "The impossibility of proving a negative is proverbial, but my opponent declares that his negative—the uselessness of specific characters—wants no proving, but must be accepted till in every case the affirmative is proved." Now, I have made no such declaration. My statement was: "It is too large a demand to make upon our faith in natural selection to appeal to the argument from ignorance, when the facts require that this appeal should be made over so large a proportional number of instances." It is really Mr. Wallace who declares that his *affirmative*—the *invariable* usefulness of specific characters—wants no proving, but must be accepted till in every case the negative is proved, notwithstanding that, as he allows, "the impossibility of proving a negative is proverbial." Of course, *if it has been previously assumed* that natural selection is the *only* factor of organic evolution, we are entitled to conclude that the doctrine of utility as universal requires no further proof, since it follows deductively from the assumption. But where the very question in dispute is as to the validity of this assumption, it becomes an almost comical instance of circular reasoning to construct our biological catechism thus:—Why do you believe that natural selection is the only factor of organic evolution? Because I know that in organic Nature utility is universal. But how do you know this, seeing that "our extreme ignorance" renders it impossible to suggest, in a vast number of cases, what the utility can be? Because I have already proved that natural selection has been the only factor at work.

(4) Mr. Wallace imports from the monthly periodicals part of our discussion on the swamping effects of intercrossing. Here therefore, I must follow him. In my Linnean Society paper I had urged that natural selection must be seriously handicapped in its action by the swamping effects of fortuitous variations intercrossing with their parent forms. This statement Mr. Wallace contradicted on the ground that Mr. J. A. Allen had furnished "a complete demonstration of individual and simultaneous variability by a series of minute comparisons and measurements," with the result of showing that, whatever modification might be required, "we *always* (italics his) find a considerable number, say from 10 to 20 per cent. of the whole, varying simultaneously, and to a considerable amount, on either side of the mean value." Now, in my reply I pointed out that all the variations thus recorded by Mr. Allen were of a kind which had "nothing to do with the difficulty," seeing that they had reference only to such features as "size, strength, fleetness, colour, relative proportions of different parts, and so on, all of which—as we well know without going beyond the limits of our own species—are so highly variable as never all to be precisely the same in any two individuals." Then, by way of illustration, I said: suppose "it were required to produce a breed of race-horses with horns upon the frontal bone, . . . or a fighting spur on a duck, clearly it could not be done by natural selection alone" in the latter case, or by artificial selection in the former; the principle of selection would here require to be assisted by "some common cause [of variation] acting on a number of individuals simultaneously." But there was nothing in the use of this illustration to provoke the remark that it indicates "the belief, apparently, that these are a class of characters which are distinctive of closely allied species"—although such does happen to be the case as regards certain allied genera. I merely requested Mr. Wallace to show me his "considerable number of specimens diverging from the mean condition," as regards either of these structures, *however incipient*—or as regards any other structures, save those the general variability of which as to relative size, &c., no one would dream of disputing. And this I still hold he is obviously bound to do, if he is to sustain his sweeping statement that whatever modification of type may be required, we *always* find from 10 to 20 per cent. varying in the needful way. Thus, as a mere matter of dialectic, I confess it appears to me a somewhat unaccountable expedient to affirm that my *reductio ad absurdum* is "preposterous"—such happening to be the very quality which this mode of refutation is ordinarily designed to present.

(5) Lastly, my critic says:—"The argument to show that the supposed physiological variations would be perpetuated, seems to me as weak and unsatisfactory as ever." This may well be. Indeed, I never supposed that anything would be likely to influence the judgment of Mr. Wallace where natural selection is concerned. But I did not write with any such object. I wrote merely to dispose of a particular criticism which he had advanced, and there can be no two opinions as to the result. For I have shown that whatever may be thought about the truth or falsehood of my theory,[1] at least it is certain that it *cannot* be affected by the criticism of Mr. Wallace; and this for the simple reason that he has run a tilt, not against my theory at all, but against a completely different theory, which, like a figure of straw, he had himself set up. Now that he can no longer have any doubt as to what my theory is, I willingly conclude that he must still have some reasons for thinking it improbable that the supposed physiological variations (if they occur) should be perpetuated. But I am free to confess that it passes my powers of conception to divine what these

[1] By a curious and undesigned coincidence, the same issue of NATURE which contains Mr. Wallace's letter also contains my review of Mr. Spencer's essay on the "Factors of Organic Evolution." In that review several other passages are quoted from Mr. Darwin's works to the same effect.

[1] I call it my theory, because I now understand that it differs widely from that of Mr. Catchpool (see NATURE, vol. xxxiv. p. 617).

reasons can be: I only know that they must be of a totally different order from those which constituted the substance of his published criticism.

Of course the question whether or not these physiological varieties *do* occur is quite distinct; and I most heartily agree with Mr. Wallace that this is a question of fact which ought to be decided, before it can be worth anybody's while to attack my suggestion upon any other grounds. If Mr. Wallace had seen this in the first instance, he might have saved both himself and me a good deal of trouble; but at the same time he would have deprived me of no small amount of encouragement. For I am now more than ever satisfied that the suggestion does not admit of being assailed on any grounds of general reasoning; but, on the contrary, that as a theory it is antecedently probable, and can only be refuted—if it is to be refuted—by an appeal to fact in the form of experiment. And as I cordially hope that this may be the last time that I shall have to address you upon this subject, I should like to neutralise the discouraging influence on experimental verification which may have been exercised by premature criticism in your pages. This I hope in some measure to effect by making two remarks. The first is that my own estimate of the antecedent probability of the theory is shared by some of the highest "authorities" on the Continent. The second is that, in all the lines of inquiry hitherto pursued, I find striking evidence of the actual occurrence of the physiological varieties in question. But as this evidence requires to be largely supplemented by experiment, and as every experiment requires at least three years to perform, those biologists who think with Mr. Wallace may be glad to hear that it will be a very long time before I shall have occasion again to trouble them with the theory of physiological selection.

GEORGE J. ROMANES