PHYSIOLOGICAL SELECTION.

SEVERAL months ago I read a paper before the Linnæan Society which was intended to convey 'an additional suggestion on the origin of species.' The hypothesis which was there sketched in outline I called Physiological Selection, and stated that my object in publishing it was merely that of inducing other naturalists to co-operate with me in what could not but prove a highly arduous work of verification. The effect of this paper, however, has been to arouse a storm of criticism, in which the critics appear to have overlooked the fact that my idea was put forward only as a 'suggestion,' or 'provisional hypothesis;' and, therefore, that in treating it as a fully elaborated theory they were investing it with a dignity it did not deserve. Nevertheless, as the result of reading these criticisms has been to make me think more highly than ever of the probability of the suggestion, and as they appear to be now exhausted, the time has come when it seems desirable that I should furnish a general answer. For if the criticisms are allowed to pass without notice from me, the impression may go abroad that the suggestion has been tried and found wanting: naturalists, therefore, may not care to undertake the labour of testing an hypothesis which they understand to have been shown antecedently improbable; and thus the only purpose which I had in publishing the hypothesis at this juncture may be frustrated. But by now furnishing a general answer to all the criticisms, I hope to show that, whether or not the hypothesis is true, at any rate it certainly has been in no way weakened by the sundry assaults to which it has been exposed.

The hypothesis of Physiological Selection [1] sets out with an attempted proof of the inadequacy of the theory of natural selection, considered as a theory of the origin of species. This proof is drawn from three distinct heads of evidence:—(1) the inutility to species of a large proportional number of their specific characters; (2) the general fact of sterility between allied species, which admittedly cannot be explained by natural selection, and therefore has hitherto

[1] Since the publication of my paper my attention has been drawn to a passage in Mr. Belt's *Nicaragua*, p. 207, where the hypothesis is foreshadowed; and also to a letter in *Nature*, vol. xxxi. p. 4, by Mr. Catchpool, where its leading principles are clearly stated.

never been explained; (3) the swamping influence, upon even useful variations, of free intercrossing with the parent form. On account of these three cardinal difficulties against the theory of natural selection, considered as a theory of the origin of species, I have ventured to affirm that this theory has been misnamed. It is not in strictness a theory of the origin of *species:* it is a theory of the cumulative development of *adaptations*. These two things are plainly very far from being the same. On the one hand, a *large proportional number* of specific characters—including the most general characteristic of mutual sterility—present no utility that can be assigned; while, on the other hand, the *immense majority* of characters which are of evident utility are the common property of numerous species. My statement, therefore, is that natural selection can only be properly regarded as a theory of the origin of species in so far as species differ from one another in regard to utilitarian structures, while at the same time failing to do so in respect of their reproductive functions. Moreover, even in such cases natural selection is only a theory of the origin of species as it were incidentally. The office of natural selection, as a principle in Nature, is in all cases that of evolving *adaptations*, whether these happen to be distinctive of species, or of genera, families, orders, &c.; and if in some cases the result of performing this office is that of raising a variety into a species, such a result is merely collateral, or in a sense accidental. Lastly, my statement goes on to show that by thus placing the theory of natural selection on its true logical footing, we are establishing it in a position of greater security than it ever occupied before; seeing that we thus release it from the three great difficulties above named—difficulties with which it has been hitherto illegitimately entangled, on account of its having been so generally regarded as exclusively a theory of the origin of species.

All this, however, is only by way of preamble to the hypothesis of physiological selection; and my object in the preamble was to show that there is a real need for some such theory of the origin of *species* as that which is afterwards rendered. The following is an outline sketch of this theory.

According to the Darwinian theory, it is for the most part only those variations which happen to have been useful that have been preserved: yet, even as thus limited, the principle of variability is held able to furnish sufficient material out of which to construct the whole adaptive morphology of nature. How immense, therefore, must be the number of unuseful variations! Yet these are all, for the most part, still-born, or allowed to die out immediately by intercrossing. Should such intercrossing be prevented, however, there is no reason why unuseful variations should not be perpetuated by heredity quite as well as useful ones when under the nursing influence of natural selection—as, indeed, we see to be the case in our domesticated productions. Consequently, if from any reason a section of a species is prevented from intercrossing with the rest of its species, new varieties of a trivial or unuseful kind might be expected to arise within that section. And this is just what we find. Oceanic islands, for example, are well known to be extraordinarily rich in peculiar species; and this can best be explained by considering that a complete separation of the fauna and flora on such an island permits them to develop varietal histories of their own, without interference by intercrossing with their originally parent forms. We see the same principle exemplified by the influence of geographical barriers of any kind, and also by the consequences of migration. Therefore, given an absence of overwhelming intercrossing, and the principle of what I term *independent variability* may be trusted to evoke new species, without the aid of natural selection.

Were it not for the very general occurrence of some degree of sterility between even closely allied species, and were it not also for the fact that closely allied species are not always—or even generally—separated from one another by geographical barriers, we might reasonably attribute all cases of species-formation by independent variability to the prevention of intercrossing by geographical barriers or by migration. But it is evident that these two facts can no more be explained by the influence of geographical barriers, or by migration, than they can be by the influence of natural selection.

Now, of all parts of those variable objects which we call organisms, the most variable is the reproductive system; and the variations may be either in the direction of increased or of diminished fertility. Consequently, variations in the way of greater or less sterility frequently take place both in plants and animals; and probably, if we had adequate means of observing this point, we should find that there is no variation more common. But, of course, whenever it arises—whether as a result of changed conditions of life, or, as we say, spontaneously—it immediately becomes extinguished, seeing that the individuals which it affects are less able (if able at all) to propagate the variation. If, however, the variation should be such that, while showing some degree of sterility with the parent form, it continues to be as fertile as before within the limits of the varietal form, it would neither be swamped by intercrossing nor die out on account of sterility.

For example, suppose the variation in the reproductive system is such that the season of flowering or of pairing becomes either advanced or retarded. Whether this variation be 'spontaneous,' or due to change of food, climate, habitat, &c., does not signify. The only point we need attend to is that some individuals, living on the same geographical area as the rest of their species, have demonstrably varied in their reproductive systems, so that they are perfectly fertile *inter se*, while absolutely sterile with the rest of their species. By inheritance there would thus arise a variety living on the same geographical area as its parent form, and yet prevented from intercrossing with that form by a barrier quite as effectual as a thousand miles of ocean; the only difference would be that the barrier, instead of being geographical, is physiological. And now, of course, the two sections of the physiologically divided species would be able to develop independent histories of their own without intercrossing; even though they are living together on the same geographical area, their physiological isolation would lead to their taking on distinct specific characters by independent variation, just as is the case with sections of a species when separated from each other by geographical isolation.

To state this suggestion in another form, it enables us to regard many, if not most, species as the records of variations in the reproductive systems of ancestors. When variations of a non-useful kind occur in any of the other systems or parts of organisms, they are, as a rule, immediately extinguished by intercrossing. But whenever they happen to arise in the reproductive system in the way here suggested, they must tend to be preserved as new natural varieties, or incipient species. At first the difference would only be in respect of the reproductive systems; but eventually, on account of independent variation, other differences would supervene, and the new variety would take rank as a true species.

The principle thus briefly sketched in some respects resembles, and in other respects differs from, the principle of natural selection, or survival of the fittest. For the sake of convenience, therefore, and in order to preserve analogies with already existing terms, I have called this principle Physiological Selection, or Segregation of the Fit.

Let it be noted that we are not concerned either with the causes or the degrees of the particular kind of variation on which this principle depends. Not with the causes, because in this respect the theory of physiological selection is in just the same position as that of natural selection; it is enough for both that the needful variations are provided, without its being incumbent on either to explain the causes which in all cases underlie them. Neither are we concerned with the degrees of sterility which the variation in question may in any particular case supply. For whether the degree of sterility with the parent form be originally great or small, the result of it will be in the long run the same; the only difference will be that in the latter case a greater number of generations would be required in order to separate the varietal from the parent form.

The object of this paper being that of furnishing a general answer to criticisms on the hypothesis of physiological selection, I will not occupy space by detailing evidence of that hypothesis, further than is needful for the object just mentioned.[2] This evidence abundantly proves that the particular kind of variation which the theory of physiological selection requires does take place, (*a*) in individuals, (*b*) in races, and (*c*) in species. Next, the evidence goes on to show that the facts of organic nature are such as they ought to be, supposing it true that this variation has played any considerable part in the differentiation of specific types. In particular, it is shown that the general *association* between the one primary, or relatively constant, specific distinction (mutual sterility) and the innumerable secondary, or relatively variable, distinctions (slight morphological changes which may affect *any* parts of *any* organisms) of itself indicates that the former has been the original condition to the occurence of the latter in all cases where free intercrossing has not been otherwise prevented. For even in cases where the secondary distinctions may be supposed to have induced the primary—or where morphological changes taking place in other parts of an organic type have exercised a reflex influence on thc reproductive system, such that the changed organism is no longer fertile with its unchanged parent form—even in such cases the theory of physiological selection is available to explain the association in question. For even in these cases, notwithstanding that the secondary changes are historically the prior changes, they still depend for their preservation on the principles of physiological selection. In other words, these principles have, in all such cases, *selected* the particular kinds of secondary distinction which have proved themselves capable of so reacting on the reproductive system as to bring about the primary distinction, and thus to protect themselves against the destructive power of free intercrossing.

I have now said enough to convey a fairly adequate idea of what the theory of physiological selection is, or enough, at all events, to render intelligible the following criticisms, which it is now my object to dispose of.

First, as to the name which I have given the theory, several critics have complained that it ought to have been called 'physiological isolation.' This is a point of no real importance, and I readily concede that in some respects physiological isolation would be a better name than physiological selection. The reasons which inclined me to adopt the latter in preference to the former will be gathered from what has just been said. If the theory is sound at all, a process of true survival takes place, in some cases of the primary, in other cases of those secondary specific characters which are capable of inducing the primary; and in either event it is only certain

[2] The evidence, so far as yet published, may be read by anyone who cares to purchase the original paper, which can be obtained from the Linnæan Society in a separate form.

changes of character, or particular variations, which are *selected* to survive as new species. Moreover, the term physiological selection does not exclude the term physiological isolation, any more than the term natural selection excludes the term survival of the fittest.

Coming now to criticism of a substantial kind, for the sake of brevity I will not recapitulate answers already given in *Nature*, and in cases where different critics have urged the same objections I will consider the latter as they are presented most fully. Moreover, I will not occupy space by considering criticisms of a puerile character —such as one that appeared in the *Athenæum*. By means of these limitations I can afford to avoid mentioning any of my critics save two, and yet not avoid meeting any of the criticisms which have hitherto remained unanswered.

Inutility of Specific Characters.—Mr. A. R. Wallace is highly indignant with the portion of my paper which deals with this subject. Both in the *Fortnightly Review* and in *Nature* he represents my views upon it as those of a heretic; and a single passage will serve to show the vigour of his scourging.

> 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.

Here we have a question of very much wider importance than that as to the truth of my theory. Indeed, this question only touches that theory in the same way as it touches the doctrine of the differentiation of species under geographical isolation. Moreover, the theory might be equally true whether or not specific characters are likewise universally adaptive characters; for it would still be available to explain the general fact of specific sterility, which the theory of natural selection is confessedly unable to explain. But, on account of the wider interest attaching to the question thus raised, I will consider at some length what appears to me an astonishing expression of opinion on the part of Mr. Wallace.

It has already been observed that, according to my argument, the theory of natural selection is a theory of the accumulative development of *adaptations* (whether these happen to be distinctive of species, genera, families, or higher taxanomic divisions), and therefore that it is only a theory of the original of *species* as it were incidentally, or so far as species differ from one another in regard to adaptive structures, and fail to do so in respect of reproductive functions. (For the sake of argument—but for this sake alone—I will here neglect the latter point.) This is what my critic calls an 'extraordinary statement,' and one which represents Mr. Darwin as having been 'during his whole life mistaken in supposing his theory to be a theory of the origin of species.' Mr. Wallace, then, does not recognise this distinction; he regards the origin of species as indistinguishable from the origin of adaptations, or in other words, that species always and only differ from one another in respect of structures that are of adaptive meaning. For the sake of brevity I will call this the doctrine of utility as universal—a doctrine which is thus set forth at the end of his long disquisition on the subject in the *Fortnightly Review.*

I believe, therefore, that the alleged inutility of specific characters claimed by Mr. Romanes as one of the foundations of his new theory, has no other foundation than our extreme ignorance, in the great majority of cases, of the habits and life-histories of the several allied species, the use of whose minute but often numerous differential characters we are therefore unable to comprehend.

Well, in the first place, this doctrine of utility as universal was certainly not countenanced by Mr. Darwin, as a single quotation will be sufficient to show:—

I now admit, after reading the essay by Năgeli on plants, and the remarks recently made by various authors with respect to animals, more especially those recently made by Professor Broca, that in the earlier editions of my 'Origin of Species' I perhaps attributed too much to the action of natural selection, or the survival of the fittest. I have altered the fifth edition of the 'Origin' *so as to confine my remarks to adaptive changes of structure*, but I am convinced, from the light gained during even the last few years, that very many structures which now appear to us useless, will hereafter be proved to be useful, and will, therefore, come under the range of naturel selection. Nevertheless, I did not formerly consider sufficiently the existence of structures, which, so far as we can at present judge, are neither beneficial nor injurious; and this I believe to be one of the greatest oversights as yet detected in my work.[3]

The words which I have printed in italics serve to show that 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 in this matter I claim to be on the side of Mr. Darwin, and certainly have nowhere made the 'extraordinary statement' that he was all his life mistaken as to the bearings of his own theory. 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 useless will hereafter be proved to be useful. But with him also I believe that a large proportional number

[3] *Descent of Man*, p. 61. The passage goes on to explain how he was led to the 'tacit assumption that every detail of structure, excepting rudiments, was of some special, though unrecognised service,' and concludes by remarking that 'anyone with this assumption in his mind would naturally extend too far the action of natural selection.' For other passages to the same effect, see *Origin of Species*, 6th edit. pp. 171, 176, 421. He is careful to affirm and to re-affirm that in the earlier editions he had 'underrated the frequency and importance of modifications due to spontaneous variability,' by which he means useless characters.

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.'

And not only have I on my side the assuredly competent—not to say magnificently candid—judgment of Mr. Darwin: I have on my side the judgment of the whole body of evolutionists without any exception, so far as I know, save that of Mr. Wallace himself. But, to give only one example, another of my critics, whose opinion upon this point must be regarded as one of the best than can be taken, remarks:—

> Another difficulty is stated to be 'that the features which serve to distinguish allied species are frequently, if not usually, of a kind with which natural selection can have had nothing whatever to do.' I fully admit the truth of the statement; and I presume that few naturalists would be prepared to deny that 'distinctions of specific value frequently have reference to structures which are without any utilitarian significance.'[4]

So that 'the alleged inutility of [many] specific characters claimed by Mr. Romanes as one of the foundations of his new theory,' is an inutility which I am not alone either in alleging or in claiming. Nevertheless, seeing that, quite apart from the theory of physiological selection, there is here a difference of no small interest between the views of Mr. Wallace and those of evolutionists in general, I will briefly consider the arguments which he sets forth in favour of his own opinion.

Observe, in the first place, he himself affirms in the passage above quoted, that, as regards structures of only specific value, it is '*in the great majority of cases*' that no utility can be suggested; but he argues that this is so only because of 'our extreme ignorance' of the life-histories and habits of the species presenting them. Now this, as shown in my paper, is the true 'argument from ignorance.' Yet Mr. Wallace borrows the phrase, and says it is *I* who have employed the argument from ignorance when I point to all the multitude of apparently useless structures and ask, What are their uses? Well, let your readers judge between us.

If it has been previously assumed that all changes of specific type have probably been due to natural selection, then, indeed, my critic might properly affirm that my 'argument from ignorance is a very bad one;' for I should then be arguing from ignorance of utility presumably present. But seeing that the very question in dispute is as to the truth of this assumption, I must deny having employed any argument from ignorance at all. My contention is that 'in a large proportional number of cases' (I do not go so far as to say 'in the great majority of cases') there *is* no utility of which to *be*

[4] *Physiological Selection*, by Henry Seebohm. (R. H. Porter, 6 Tenterden Street.)

ignorant. Clearly, therefore, it is Mr. Wallace who employs the argument from ignorance when, as a deduction from his theory of natural selection applied in all cases, he affirms that any character apparently useless *must* nevertheless be useful, and that the only reason why it appears useless is because of 'our extreme ignorance' of its utility.

Furthermore, this kind of argument amounts to nothing better than reasoning in a circle. For the evidence that we have of natural selection as an active principle in Nature is furnished by the observed utility of innumerable structures; therefore, unless we reason in a circle, it is not competent to argue that all apparently useless structures are due to natural selection acting through some kind of utility which we are unable to perceive. The case, no doubt, would be different if the great majority of specific distinctions were of any assignable use. But it is too large a demand 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.

To this Mr. Wallace rejoins with a large enumeration of instances *per contra*—particularly such as serve to illustrate the now familiar principles of protective colouring, adaptations of flowers to fertilisation by insects, &c. But in all these pages he is merely beating the air, without in any way touching me. I have never disputed the truth of any one of these principles, and no one can entertain a greater appreciation of the success with which they have been so largely established by the celebrated labours of my critic. He appears, however, to have forgotten that the only question between us is concerning the justification of his assumption of utility as *universal.* The burden of proof lies with him to justify his assumption; and this he cannot do by a mere appeal to the argument from ignorance, or by saying—I have shown you the use of some specific characters, therefore you must believe in a use for all specific characters, no matter how far you may have to stretch your powers of credence. As a matter of logic we might as well argue that because a great many deaths can be proved to be caused by railway accidents, therefore death cannot take place in any other way; and hence that, in all cases of death from unknown causes, the agency of railway accidents must be invoked, because to question this must be to make a bad use of the argument from ignorance. Doubtless other causes of death besides railway accidents are *known*; but so likewise are known other causes of specific change besides natural selection, such as sexual selection, use and disuse, correlated variation, &c. And if it be true that we know *more* about the causes of death than we do about the causes of specific change, this only tells against the attribution of all those changes whose causes we do not know to one of the causes which we do.

Again, there is a positive evidence to show that the slight changes of form and colour which chiefly serve to distinguish allied species are often due to what Mr. Darwin calls 'the direct action of external conditions,' such as changes of food, climate, &c., as well as to mere independent variation on isolated areas, and in some of our domesticated productions, &c.; and in none of these cases do the specific changes which result present a meaning of any kind.[5]

On the whole, then, I submit that Mr. Wallace's criticism thus far is a failure. It is not to be expected that evolutionists will follow the circular reasoning from utility to natural selection in some cases, and back again from natural selection to utility in all other cases. Be it observed, this great assumption of natural selection as the sole cause of specific differentiation—and, therefore, of utility as universal —is in no way necessary to the theory of natural selection; it is merely a gratuitous dogma attached to that theory, serving but to encumber its evidence, and so to cast discredit on the whole. For it is everywhere refuted by facts, was expressly rejected by the matured judgment of Mr. Darwin, and as now reconstructed by Mr. Wallace stands like the feet of clay in a figure of iron.

Sterility between Species.—Under this head Mr. Wallace's criticism amounts to nothing more than a vague suggestion to the effect that all other naturalists may have hitherto exaggerated the generality of some degree of sterility between species. But as he allows that it is 'a

[5] For instance, Mr. Wallace lays special stress on colour, arguing that no matter how small the difference of colour may be between two allied species, the difference *must* be attributed to natural selection, even though we may be quite unable to suggest in what way so small a difference can be of any conceivable use. But we know for a fact that even in a single generation very great changes of colour may be produced by the direct action of changed conditions of life. For example, Mr. Seebohm tells us, in his paper on Physiological Selection, that 'if a canary be fed exclusively on cayenne pepper it becomes scarlet; if a bullfinch be fed exclusively on hemp seed it becomes black.' And that any such meaningless changes of colour —induced by changes in the conditions of life—are often cumulative in successive generations, a single quotation from Darwin will be enough to show. 'Dr. Buchanan states that he has seen turkeys raised from the eggs of wild species lose their metallic tints and become spotted in the third generation. Mr. Yarrell many years ago informed me that the wild ducks bred in St. James' Park lost their true plumage after a few generations. An excellent observer (Mr. Hewitt) . . . found that he could not breed wild ducks true for more than five or six generations, as they proved so much less beautiful. The white collar round the neck of the mallard became broader and more irregular, and white feathers appeared in the duckling's wings, &c.' Mr. Darwin also remarks, 'each of the endless variations which we see in the plumage of our fowls must have had some efficient cause; and if the same cause were to act uniformly during a long series of generations on many individuals, all probably would be modified in the same manner.' The obvious truth of this remark serves to dispose of Mr. Wallace's argument in the *Fortnightly*, that 'the general constancy of colouration we observe in each wild species' of itself furnishes sufficient proof that the colouration must be 'a useful character.' Moreover, when using this argument Mr. Wallace forgets that uniformity of colouration (whether useful or unuseful) is preserved in wild species by free intercrossing. Where this is prevented —as by isolation or migration—variations of colour very frequently do take place, just as in the then analogous case of our domesticated strains.

widespread phenomenon,' and gives no reasons for differing from Mr. Darwin's careful estimate of its frequency, he does not really furnish me with any material to discuss. In seeking to establish by *à priori* considerations what the facts ought to be in order to suit his own philosophy of natural selection as ubiquitous, Mr. Wallace is as singular in his opinion on the subject of sterility as we have already seen that he is—and for the same reason—on the subject of utility.

Swamping Effects of Intercrossing:—Concerning this part of my argument, Mr. Seebohm writes:—

> This is unquestionably a very grave difficulty, to my mind an absolutely fatal one to the theory of accidental variation. . . . So far as is known, no species has ever been differentiated without the aid of geographical isolation, though evolution may have gone on to an unknown extent.

By this he means that, apart from geographical isolation, there can be no *multiplication* of species, but only a transmutation of species in linear series—such transmutation being due to some general cause acting on all the individuals of a species simultaneously. In other words, so overpowering does Mr. Seebohm regard the swamping effects of intercrossing with parent forms, that he does not deem it possible for natural selection to differentiate a specific type without the aid of isolation.

This, of course, is going much further than I have gone; and therefore, as far as my theory is concerned, I have no reason to dispute an opinion which concedes so much more than I require. Nevertheless, for the sake of the wider philosophy of evolution in general, I may remark that this extreme view touching the swamping influence of intercrossing is, in my opinion, a mistake. It is nearly the same view as was put forward with much elaboration by Moritz Wagner, in 1868.[6] By means of a large accumulation of facts—which are certainly of value as showing the importance of isolation in the differentiation of species—Wagner thought he had proved the impossibility of natural selection producing a transmutation of species without the assistance of isolation. Subsequently, however, Weismann completely exploded this theory by bringing it to the test of another class of facts.[7] Hilgendorf had published a remarkable essay on a series of fossil snails which occur in an ancient lake-basin of Steinheim.[8] This lake-basin is of small size, but extraordinarily rich in peculiar species of one genus of snail; and as these species occur one above another in successive strata, they conclusively prove the occurrence of transmutation without isolation.

And here I may remark that when we look closely into this

[6] *Die Darwin'sche Theorie, und das Migrationsgesetz der Organismus,* (Leipzig).

[7] *Ueber den Einfluss der Isolirung auf die Artbildung.* (Leipzig, 1872).

[8] *Ueber* Planorbis multiformis *im Steinheimer Susswasserkalk.* ('Monatsbericht der Berliner Akademie,' 1866.)

the most definite and beautiful record of species-formation hitherto brought to light, it appears to furnish the strongest testimony to the theory of physiological selection. The facts are these. The snail population of this lake remained for a long time uniform or unchanged. Then a small percentage of individuals suddenly began to vary as regards the form of their shells, and this in two or three directions at the same time—each effected individual, however, only presenting one of the variations. But after all these variations had begun to affect a proportionally larger number of individuals, some individuals began to occur in which two or more of the variations were blended together—evidently, as Weismann says, by intercrossing of the varieties so blended. Later still, both the separate variations and their blended progeny became more and more numerous, and eventually a single blended type, comprising in itself all the initial varieties, supplanted the parent form. Then another long period of stability ensued, until another eruption of new variations took place, and these variations, after having affected a greater and greater number of individuals, eventually blended together by intercrossing, and supplanted their parent form. So the process went on —comparatively short periods of variation alternating with comparatively long periods of stability—the variations, moreover, always occurring suddenly in crops, then multiplying, blending together, and in their finally blended type eventually supplanting their parent form.

Now, the remarkable fact here is that each time when the variations arose, they only intercrossed between themselves; they did not intercross with their parent form; for, if they had, not only could they never have survived (having been at first so few in number, and there having been no geographical barriers in the small lake), but we should have found evidence of the fact in the half-bred progeny. Moreover, natural selection can have had nothing to do with the process, because not only are the variations in the form of the shells of no imaginable use in themselves; but it would be simply preposterous to suppose that at each of these 'variation-periods' several *different* variations should *always* have occurred *simultaneously*, all of which were of some *hidden use*, although no one of them ever occurred during any of the prolonged periods of stability. How, then, are we to explain the fact that the individuals composing each crop of varieties, while able to breed amongst themselves, never crossed with their parent form? These varieties, each time that they arose, are found closely commingled with their parent form, and would certainly have been reabsorbed into it had intercrossing in that direction been possible. I conclude, therefore, that there is only one conceivable answer to my question. Each crop of varieties must have been *sexually protected* from intercrossing with their parent form. They must have been the result of a sexual variation occurring at first in a few individuals, rendering these individuals sterile with their parent form, whilst leaving them fertile amongst themselves. The progeny of these individuals would then have dispersed through the lake, physiologically isolated from the parent population, and especially prone to develop secondary variations as a direct result of the primary or sexual variation.[9] Thus, as we might expect, two or three varieties arose simultaneously (as expressions of so many different lines of family descent from the original or sexual variety): these were everywhere prevented from intercrossing with their parent form, yet capable of blending whenever they, or their ever-increasing progeny, happen to meet. Thus, without going into further details, we are able by the theory of physiological selection to give an explanation of all these facts, which otherwise remain inexplicable.

But to return to my critics. I will next consider Mr. Wallace's objection to my views upon the swamping effects of intercrossing. Here he summarises his whole criticism thus:—

> 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 in natural history.

Now, first of all, if this alleged fact is 'one of the best established facts in natural history,' my readers must have been somewhat surprised to find so accomplished a naturalist as Mr. Seebohm displaying so sublime an ignorance of its establishment. For we have just seen that he goes very much further than I have gone in his appreciation of this difficulty from intercrossing. Therefore in this matter I occupy an intermediate position between my two critics. On the one hand it is represented that I am unaware of one of the most 'general' and 'best established' facts in natural history. On the other hand, it appears that 'Mr. Romanes has done great service in calling attention to the swamping effects of free intercrossing:' that, especially on this account, 'the paper by Mr. Romanes is a very valuable contribution to the literature of evolution,' seeing 'it is seldom that the difficulties of natural selection from fortuitous variations have been so clearly, so impartially, but so candidly, set forth. In a word, upon this matter of intercrossing, just as in the previous matter of inutility, my two most authoritative critics take precisely opposite views. This perhaps may serve to show my readers, better than anything that I can say, the nett value of their criticisms. But,

[9] See p. 399 of my Linnæan Society paper, where it is shown that any variation in the reproductive system is apt to entail morphological changes in the progeny.

all the same, I will briefly answer the somewhat oracular utterance of Mr. Wallace.

According to this utterance it would appear that 'one of the best established facts in natural history' is standing, like an inverted pyramid, upon the basis supplied by the observations of an American naturalist, Mr. Allen. At all events, this is the only work which Mr. Wallace quotes to show how securely the fact in question is established. Now, this work is well known to all evolutionists, and while there is no doubt about its valuable character, I should be surprised if Mr. Wallace could quote any evolutionist who would agree with him in maintaining that it is in itself sufficient to close so very large and complex a question as that concerning the resultant between the opposing forces of natural selection and free intercrossing. Mr. Allen's results, which are somewhat needlessly quoted in the *Fortnightly Review*, 'establish' the following proposition as regards certain species of birds, namely, 'that a variation of from fifteen to twenty per cent. in general size, and an equal degree of variation in the relative size of different parts, may be ordinarily expected among specimens of the same species and sex, taken at the same locality.' These are the 'facts' upon which Mr. Wallace relies as final and conclusive proof that natural selection is in no way incommoded by free intercrossing, and therefore can work out all specific changes without the need of any aid from the principle of isolation. Although in the opinion of so learned an ornithologist as Mr. Seebohm no one species is known to have been differentiated by natural selection without such aid, Mr. Wallace triumphantly points to this certainly not obscure work of Mr. Allen as a kind of short and easy way with the sceptics: 'we have no longer any occasion to reason as to what kind or amount of variation is probable, since we have accurate knowledge of what it is.' Possibly this knowledge may turn out to be a little too accurate for the large and general doctrine which Mr. Wallace rears upon it. Let us see.

Variations of the kind with which Mr. Allen's measurements are concerned have nothing to do with the difficulty against natural selection which arises from the swamping effects of free intercrossing. For this objection applies only to the cases of so-called 'accidental' variations, and even here only to cases where such variations are necessarily rare. In all cases where similar variations are numerous and simultaneous, the difficulty, of course, does not apply; for if they also happen to be useful, natural selection may then have sufficient material wherewith to overcome the adverse influence of free intercrossing. Variations may be similar, numerous, and simultaneous, either on account of *some common cause acting on a number of individuals simultaneously*, or on account of *the structures in question being more or less variable in all directions round a specific mean.*

Now, the variations which were studied by Mr. Allen are all of this latter class, and so resemble the variations on which the 'unconscious selection' of man is able to operate when progressively improving, say, a breed of racehorses. In neither case are the variations of a kind out of which it could be possible for selection to evolve a *new structure*. The only features which here admit of any alteration at the hands of selection are features which already exhibit a considerable amount of variation round an average mean. Of such features are size, strength, fleetness, colour, relative proportion 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. Hence I should deem it mere folly in any one to question that it is an easy thing for unconscious selection under domestication, or for natural selection under Nature, gradually to 'improve' such features, should either an exaggeration or a diminution of any one of them happen to become desirable. But were it required, for instance, to produce a breed of racehorses with horns upon the frontal bone, no amount of unconscious selection could ever do it. And similarly with Mr. Allen's birds. It is easy to see how natural selection could alter the general size of the body, the relative sizes of parts, degrees of colouration, &c., without encountering any great difficulty from intercrossing. But if it were required to produce, say, a fighting spur on a duck, clearly it could not be done by natural selection alone, or when depending only on 'accidental variations.' In all such cases (*i. e.* where the features to be modified are not already variable round the specific mean), selection of either kind can only begin to act when it ceases to depend on chance variations—that is, when variations of the particular kind required are supplied by some determining cause acting upon a number of individuals simultaneously. Yet Mr. Wallace maintains that *whatever* modification may be required, 'we *always* find a considerable number —say from ten to twenty per cent. of the whole—varying simultaneously, and to a considerable amount, on either side of the mean value'!

The Theory of Physiological Selection.—So much, then, for Mr. Wallace's counter-criticisms on my criticism of the theory of natural selection, considered as *in itself* a sufficient theory of the origin of *species*. It remains to consider the exceptions which have been taken more especially to the theory of physiological selection. And here, for the first time, we find Mr. Wallace in agreement—or rather not in flat contradiction—with Mr. Seebohm. But before considering their common criticism, I should like to call attention to the following concessions on the part of Mr. Wallace.

He 'fully admits that variations in fertility are highly probable;' 'that individual variations occur which, while infertile with some members of the same species, are fertile with others;' and, therefore, 'that varieties which exhibit no other distinctive character than sterility with the bulk of their species may arise.' He only 'claims to have shown that these varieties are at an immense disadvantage, and could hardly by any possibility be preserved and increased till they were required to form the nucleus of a new species.'

Thus much, then, is conceded even by this the most hostile of my critics. My 'statement, with the results deduced from it, sounds feasible,' he says; but 'when closely examined,' is seen to 'slur over insuperable difficulties.'

Well, what other difficulties there may be I know not; but it is certain that Mr. Wallace has thought fit to adduce only one. This one difficulty is that the chances must be greatly against the 'physiological complements' (or the two suitably varied individuals of opposite sexes) happening to mate. Moreover, even if the lucky chance were to occur, it would require to occur again between some of the progeny resulting from the union, before a sufficient number of suitably varied individuals could be born to start a permanent variety. This, as I have said, is the one consideration upon which Mr. Wallace—and also Mr. Seebohm—stakes his whole opinion.

First of all, then, and for the sake of argument, I will 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 the area occupied by a large species. I will not wait to dwell upon the fact that his remarks apply only to species which are *unisexual*, or that even as regards these the force of his objection is diminished if applied to unisexual species which are also *polygamous*. These minor points may be neglected, and I agree that, under the circumstances supposed, the variation in question, 'whenever it occurs, is almost certain to die out immediately.'

Having reached this conclusion—inevitable from his premisses—Mr. Wallace imagines that he has disposed of the whole business. 'I have shown,' he says, 'by considering carefully the results of the variations suggested by Mr. Romanes, that they could not possibly produce the effects which he attributes to them.' Now, on my side I will show that his consideration has not been sufficiently careful to take cognisance of two important facts, either of which alone is enough to shatter a criticism that amounts to little more than the announcement of a truism.

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.[10] Whether or not it is a matter of chance will depend on the causes which determine the variation. When these

[10] For example, after rendering evidence of 'individual incompatibility,' or of the sporadic occurrence of sexual variations in two individuals only, the paper proceeds as follows, excepting, of course, the italics.

'But of even *more* importance to us is the direct evidence of such a state of matters in the case of *varieties*, *breeds*, or *strains*. Incompatibility between individuals is, indeed, of very great importance to my theory, because it constitutes the first link in a chain of direct evidence as to the actual occurrence of the particular kind of variation on which the theory depends; here we have, as it were, the first beginning in an individual organism of a change which, *under suitable conditions*, may give rise to a new *strain*, and so eventually to a new species. But, *seeing that the individual is so small a constituent part of his species*, unless his peculiar incompatibility has reference to the *majority* of other individuals, so that it becomes only the *minority* of 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 in 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.[11]

the opposite sex with whom he can pair, the *probability* is that the peculiar condition of his reproductive system would *not* be perpetuated by heredity, but would become extinguished by intercrossing. As I have already said, it is, physiologically considered, even more remarkable that such incompatibility should ever be *exclusively individual* than it should be *racial*; and, therefore, as likewise remarked, I regard these cases of individual incompatibility as of value to my theory *chiefly* because they prove the actual occurrence of the variation which the theory requires, and this as *suddenly* or *spontaneously* arising in the highest degree of efficiency. But I will now adduce evidence to show that a state of matters more or less similar may be proved to obtain throughout a whole *breed* or *strain*, so that we then have, not merely *individual* incompatibility, but what may be termed *racial* incompatibility; *and, therefore, that we are on the high road to the branching-place of a new species.*'

I can only suppose that this passage, as well as others to the same effect, must have entirely escaped the notice both of Mr. Wallace and Mr. Seebohm.

[11] Perhaps it is not wholly needless to point out that I am guilty of no inconsistency when thus arguing for a 'collective variation' on the part of the reproductive system, after having urged the difficulty against natural selection which arises from free intercrossing—i. e. the difficulty of supposing that a sufficient number of variations of the same kind should always be forthcoming simultaneously to enable natural selection to overcome the influence of free intercrossing. For, as previously explained, this objection is only valid in the case of 'accidental,' 'sporadic,' or 'spontaneous' variations, which, *ex hypothesi*, are relatively very few in number. The objection does not apply to 'collective variations,' which, being due either to a common cause or to general variability of size, &c., about a mean, affect a number of individuals simultaneously. But, in whatever measure collective variations are

And here, curiously enough, Mr. Wallace comes forward with an additional suggestion under this head, which, however, he regards as an 'alternative hypothesis.' This additional suggestion is that there may be a connection between sexual compatibility and external colouring, such that any variation in the latter may be accompanied by a correlated variation in the former, leading to sterility with the unmodified, or differently modified, type of colour. So that when colour is changed, for protective or other purposes, by natural selection, an indirect or incidental change may be wrought in the reproductive system, such that the modified individuals are fertile only amongst themselves. Now, for reasons mentioned below, this hypothesis does not recommend itself to my mind as at all likely to be 'the true solution of the problem of the sterility of hybrids.'[12] It may possibly be a true explanation of some cases; but to regard it as probably the true explanation of all appears to me absurd. However, the point with which I am concerned is not as to the validity of this suggestion in itself, but merely with the astonishing misapprehension of my theory which leads Mr. Wallace to regard the suggestion as an 'alternative hypothesis.' Far from being in any way opposed to my theory, his suggestion runs directly on its lines; he merely seeks to add another to the many causes of the indirect class on which I myself rely. As clearly explained in my paper, it makes no difference

induced by any cause acting directly on a specific type, in that measure is the indirect action of natural selection superseded by the independent principles of what Mr. Spencer calls 'direct equilibration.' Of course these principles may *co-operate* with that of natural selection; but none the less they are quite *distinct*. In short, my objection to natural selection on the score of free intercrossing only applies to cases of 'accidental variations,' relatively few in number; where 'collective variations' are supplied to natural selection by other causes the objection, of course, is satisfied.

[12] 1. Many species which are mutually sterile differ very little in colour.

2. Most species which are mutually fertile differ considerably in colour.

3. Our domestic varieties, both of plants and animals, are largely reared more or less expressly for the purpose of obtaining extreme differences of colour; yet nearly all the resulting varieties are notoriously fertile.

4. In the case of natural species, it often happens that a great difference in respect of fertility occurs according to which has acted as the male and which as the female; yet in both these crosses the colour of each species, is of course, the same.

5. Similar remarks apply to the case of dimorphic and trimorphic plants.

6. In the case of fertile hybrids, it may be regarded as a general rule that the more nearly they resemble either parent form in colour, the greater is their sterility.

7. Even apart from all these opposing facts, on merely antecedent grounds it is highly improbable that, to use Mr. Wallace's own words, 'so widespread a phenomenon as that of some degree of sterility between species' should be due to any merely accidental correlation between external colour and reproductive function, extending throughout the whole range of organic nature.

8. The suggestion supposes natural selection to be the cause of the colour-change. If so, in most cases the unchanged individuals must die out. How, then, does it come to pass that there continues to be an unchanged type of colour with which the changed type is now found to be infertile?

to the theory of physiological selection what the particular causes may be which induce the sexual change in any particular case; and I expressly insist that natural selection may well be regarded as one among the sundry other causes, of the indirect class which do induce this variation. These causes, both direct and indirect, I believe to be numerous, varied, sometimes complex, generally subtle, and therefore often obscure. But to take on the present occasion a merely bird's-eye-view of the matter, when we consider the extraordinary sensitiveness of the reproductive system to slight changes in the conditions of life, we cannot fail to conclude that in the long life-histories of species—furnishing great vicissitudes to large populations spread over wide areas—many and diverse causes must often be encountered, leading to collective variation on the part of this system, and that these variations must sometimes be of the kind which my theory requires.

And here it may be remarked that it was such cases as these of collective variability (or where the physiological variation required by my theory affects a number of individuals simultaneously) which I had in view while writing that such a variations 'must always be preserved whenever it occurs,' and this 'with even more certainty than are the useful variations which furnish material to the working of natural selection.' Mr. Wallace calls this a 'most extraordinary statement,' and no doubt it must have appeared so to him, seeing that he only waited to consider the case of physiological variations arising fortuitously—where, as he needlessly argues a self-evident fact, there must be many chances against even the first mating of the physiological complements. But of course the 'extraordinary' nature of my statement altogether disappears when its meaning is understood; for it is surely sufficiently evident that if the variation does not merely occur sporadically in an individual here and there, but affects simultaneously a large number of the inhabitants of a district, it is more certain to be perpetuated than any 'accidental' (even though useful) variation could be; seeing, on the one hand, that it cannot be obliterated by intercrossing, and, on the other hand, that the 'fitness' of the individuals affected is guaranteed by the fact of their having reached the breeding age. This latter point is important, because Mr. Wallace accuses me of having lost sight of the consideration that my physiological variations must conform to the law of natural selection. He says, 'Mr. Romanes' argument almost everywhere tacitly assumes that his physiological variations *are* the fittest, and that *they* always survive! With such an assumption it would not be difficult to prove *any* theory of the origin of species.' Now, I hold that this tacit assumption is justified by the consideration that if these physiological varieties ever occur at all, *ex hypothesi* they must have so far passed muster with respect to general fitness as to be allowed to propagate their kind. It was for the sake of emphasising this feature of my theory that I gave to the latter the alternative title of 'Segregation of the Fit.'

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 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 in the majority of an entire species?

GEORGE J. ROMANES.