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MR. A. R. WALLACE ON PHYSIOLOGICAL SELECTION.*

IN 1886 I published a paper entitled "Physiological Selection: an additional suggestion on the origin of species," (Zoölogical Journal of the Linnean Society, Vol. XIX, p. 337). The view there expressed is, briefly, as follows.

Given the facts of heredity and variability, the whole theory of organic evolution becomes neither more nor less than a theory of the causes which determine the breeding of like with like, to the exclusion of unlike. For the more firmly that we believe in heredity with variability as the fundamental principle of organic evolution, the stronger must become our persuasion that segregate breeding (or exclusive mating of like with like) must lead to divergence, while indiscriminate breeding (or free intercrossing of all varieties) must lead to uniformity. So long as there is free intercrossing, heredity makes in favor of fixity of type—or, at most, can permit change only in a single line, where successive generations undergo a continuous improvement, which may give rise to a

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* In a private letter to the editor of this magazine Professor Geo. J. Romanes writes: "The article refers to a completely new departure in the theory of evolution, striking in the principle of homogamy, the root-principle of the whole, and in physiological selection, one of the main branches. Yet neither principle has so far been perceived except by Mr. Gulick .... The theory of physiological selection has been better understood in America than in this country; and I should like the naturalists there, who have taken such a warm and appreciative interest in it, to see my reply to Mr. Wallace published in an American periodical."

ladder-like series of species in time. But in order that there should be a tree-like multiplication of species in space, or a simultaneous divergence of type, it is essential that free intercrossing be prevented at the origin, and throughout the development, of each branch. In other words, it is only when assisted by some form of segregation—which determines exclusive breeding of like with like—that heredity can effect arborescent or polytypic, as distinguished from catenated or monotypic, evolution. For the sake of greater clearness, I will call segregation in this sense *homogamy*, or the exclusive mating of individuals which belong to the same variety.

Now homogamy may be secured in a very great number of different ways. Of these the most important, from every point of view, is natural selection. Here the exclusive breeding of like with like is determined by general fitness, and is effected by extermination of the unlike—i. e., the comparatively unfit. Moreover, this process leads to a continuous improvement in the way of adaptation, and in this important respect it stands alone among all the forms of homogamy. Nevertheless, we must note that, unless assisted by some other form of homogamy, natural selection can only produce monotypic evolution; never polytypic. Successive generations may thus continuously mount to higher stages of adaptation on the steps supplied by their own dead selves; but although they may thus give rise to a linear series of species in time, they can never thus give rise to a multiplication of species in space. In order to effect such multiplication, or *divergence* of types, natural selection must be supplemented by some other form of homogamy, which can prevent intercrossing between the equally fit at the origin, and throughout the development, of every separate branch.

Well, as I have said, these other forms of homogamy are very numerous. First we may notice geographical isolation. When a comparatively small portion of a species is thus separated from the rest of its kind, intercrossing is effectually prevented between the two sections; and inasmuch as the general average of specific characters in the isolated section will be somewhat different from that of the other section, heredity will determine that the two sections shall not run parallel in their subsequent lines of evolutionary history: there will arise an increasing divergence between them, as was first pointed out by the mathematician Delbœuf, subsequently by the naturalist Weismann, and more recently, with greater emphasis, by Mr. Gulick as well as myself.

Again, there is homogamy that arises as a result of sexual preference, or, as I have called it, "psychological selection." It is a matter of observation that the breeding of like with like is often determined among the higher vertebrata by individuals of each variety preferring to mate with other individuals of their own variety; and this is homogamy.

Not to occupy space with any attempt at enumerating all the many forms of homogamy* I will at once pass on to the form which constitutes the subject-matter of the present paper—and the form which, in my opinion, is probably of more importance than any other in the multiplication of species. This is the form of homogamy which I have termed Physiological Selection, or Segregation of the Fit, and Mr. Gulick—who independently perceived the principle—has called Segregate Fecundity.

As my object on the present occasion is to answer criticisms which have been passed on my enunciation of this principle, I do not propose to go into further detail by way of explanation than is necessary in order to render intelligible both the criticisms and my reply thereto. Moreover, this reply is only an abstract of a fuller one which has been prepared for publication in a forthcoming book. Therefore it deals only with the main points. Lastly, I may remark that the criticisms which have hitherto appeared have all been derived from the same source, viz., from Mr. A. R. Wallace; for, although many other naturalists have expressed themselves as more or less opposed to the new theory, or "additional suggestion on the origin of species," they have all done so on the grounds, or for the reasons supplied by Mr. Wallace. Therefore, in dealing with Mr. Wallace's objections, I shall be dealing with the only objections which have thus far been advanced.

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* This has been done in a most careful and exhaustive manner by Mr. Gulick in his papers which have succeeded mine in the publications of the Linnean Society

In order at once to restate the theory of physiological selection, and to do so in a form which cannot be suspected of being in any way influenced by Mr. Wallace's more recent criticisms, I will begin by reproducing the main features of the theory in the words which were employed for this purpose more than three years ago, when I supplied an article to the *Nineteenth Century* in answer to one by him in the *Fortnightly Review*. Moreover, for the most part this restatement of the theory is quoted *verbatim* from my original paper—the differences being due only to the conditions imposed by limits of an article.

The following, then, is quoted from the *Nineteenth Century* for January, 1887:

"According to the Darwinian theory [which, as elsewhere fully explained, the present theory is in no way capable of supplanting, but only of supplementing, and this among other ways, by explaining why it is that some degree of mutual infertility is so general a phenomenon as between allied species—a phenomenon which Darwin expressly regarded as not explicable by the theory of natural selection], 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. [Homogamy.]

"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 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 one 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, etc., 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 variations, [or homogamy,] 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 tne 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. [In other words, homogamy due to such physiological isolation is cumulative.]

"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.* 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 effect *any* parts of *any* organisms), of itself indicates that the former has been the original condition to the occurrence 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 the 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

* The evidence, so far as yet published, may be read by any one who cares to purchase the original paper, which can be obtained from the Linnean Society in a separate form.

cases, notwithstanding that the secondary changes are historically the prior changes, they still depend for their preservation on the principles of physiological selection. 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."

Now for Mr. Wallace's criticism of this theory, as presented in his recently published work on "Darwinism."

Briefly put, he furnishes a numerical calculation, showing that when "the physiological peculiarity is not correlated with any external differences of form or color, or with inherent peculiarities of likes or dislikes leading to any choice as to pairing," even when so large a proportion as ten per cent. of the exceptional variety arises every year in the midst of the species, "it is unable to increase its numbers much above its starting-point, and remains wholly dependent on the continued renewal of the variety for its existence beyond a few years."

This, it must be observed, is a reproduction of the criticism which I answered in 1888; but, as Mr. Wallace ignores that answer, I must now repeat it.

The criticism does not dispute the fact that the required variation in the way of "selective sterility" occurs. Indeed, Mr. Wallace allows that it certainly must be of very general occurrence as between incipient species (or pronounced varieties in a state of nature), seeing that it is of such general occurrence as between allied species when fully differentiated as such. In other words, this variation in the way of selective sterility must be recognised as a very general *fact*, even if it be not regarded as a *condition*, or a *cause*, of specific differentiation. Which is merely another way of saying that the particular variation which is required by the theory in question is admittedly a variation which does occur; and occurs, moreover, in very frequent association with the origin of a new species. But Mr. Wallace's objection to regarding this variation as itself a cause of (or condition to) the origin of a new species is, as we have seen, that the changes must always be greatly against the similar variations of the opposite sexes meeting—i. e., of the "physiological complements" happening to pair. Now, I have already shown, in the *Nineteenth Century* of three years ago, that this criticism can only apply to species the sexes of which unite for every birth; but as Mr. Wallace continues to ignore this important consideration, I will now present it in somewhat more detail.

In considering any "supplementary theory" of the origin of species, it is obviously absurd to disregard the realm of organic nature as a whole, and to fasten attention exclusively upon the part of it where a particular difficulty against the theory may be supposed to lie. As will presently be shown, Mr. Wallace is entirely mistaken in supposing that his particular difficulty does lie against the theory in any part of organic nature; but, even if this could not have been shown, it would not have followed that the theory of physiological selection is inapplicable to *all* the classes of the animal and vegetable kingdoms, because it is taken to be inapplicable to *some*. One might just as well argue against Mr. Darwin's theory of sexual selection on the ground that it cannot be held to apply to the coloration and the sculpture of shells. If either sexual selection or physiological selection were put forward as an *exclusive* theory of the origin of *all* species, this kind of argument would, of course, have been valid; but as the matter actually stands, it is largely irrelevant.

I say *largely* irrelevant, because I do not dispute that there is this much force in it. If the theory of physiological selection can be proved inapplicable to Birds and Mammals (which are the only classes that Mr. Wallace considers in connection with it), its applicability to all other divisions, both of the animal and vegetable kingdoms, would be rendered doubtful; seeing that the process of species-formation appears to have been *everywhere* more or less associated with the occurrence of "selective sterility"; and hence, if in any division of organic nature it could be shown that selective sterility cannot possibly have been a cause of specific differentiation, we might well doubt whether it has been such a cause elsewhere—just as we may doubt whether sexual selection has been a cause of the brilliant colors of birds and butterflies, because we know, that it cannot have been a cause of the equally brilliant colors of corals and flowers. But, as far as physiological selection is concerned, no such question can arise, as I will presently proceed to show.

First of all, however, it is desirable briefly to indicate the strength of this theory in the parts of organic nature where Mr. Wallace's sole criticism cannot possibly be held to apply—viz., the larger part of the vegetable kingdom, where ovules are fertilised either by insects or by the wind. Here the phenomena of "prepotency" are highly suggestive—not to say, in my opinion, virtually demonstrative—of physiological selection; seeing that, as Mr. Darwin remarks in another connexion:

> "There can be no doubt that if the pollen of all these species (of Compositae) could be simultaneously or successively placed on the stigma of any one species, this one would elect with unerring certainty its own pollen. This elective capacity is all the more wonderful, as it must have been acquired since the many species of this great group of plants branched off from a common progenitor." *

Darwin is here speaking of elective affinity in its more fully developed form, as this so often obtains between fully differentiated species. But we meet with all lower degrees of its development—sometimes between "incipient species," or varieties, and at other times between closely allied species. It is then known as "prepotency" of the pollen belonging to the same variety, or species, over the pollen of the other variety or species, when both sets of pollen are applied to the same stigma. This is one form of what I have called physiological selection, and in my view it serves to explain why it is that hybrids between closely allied forms growing on common areas (whether they be called "species" or "constant varieties") are so comparatively rare in nature, even in cases where there is no difficulty in producing hybrids artificially by an intentional exclusion of the pollen belonging to the same form. And I allude to these facts in the present connexion for two reasons. In the first place, they serve to show how entirely irrelevant Mr. Wallace's whole criticism is to the vegetable kingdom, as well as to the majority of aquatic animals. In the next place, they serve to

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* *Variation*, etc., Vol. ii.

show how entirely unwarranted is his statement, that "we have at present no evidence whatever" in support of my belief that a physiological incompatibility may affect a whole race or strain. Not only have we the multitudinous cases of prepotency, where the incompatibility is *partial* (or in course of becoming, as Mr. Darwin says in the above quotation, "acquired"); but we have also multitudinous cases where the incompatibility has become *absolute*, both as between closely allied species, and even as between varieties of the same species growing on common areas—as M. Jordan has experimentally proved. Therefore in the above remark we have but an additional example of Mr. Wallace's entire forgetfulness, in the present connexion, of any organisms other than those which belong to the class of Birds or of Mammals.*

Turning, then, to the only parts of organic nature where his criticism can even appear to apply, I have here the sufficiently easy task of proving, that this appearance of application arises wholly and entirely out of Mr. Wallace's misapprehension of the theory against which the criticism is directed. In other words, he is not criticising the theory of physiological selection at all, but merely his own travesty of it. For, as repeatedly stated in my original paper, and again reiterated three years ago in the *Nineteenth Century*, it constitutes no part of my theory to deny the co-operation of other forms of segregate breeding or homogamy. On the contrary, I have always insisted—and Mr. Gulick has proved by calculation—that the more efficient the co-operation of other forms of homogamy, the *greater* must become the importance of the physiological form. Yet, as I trust has already been made fully apparent,

* It seems scarcely worth while to add that Mr. Wallace is doubly mistaken where he says, "Mr. Romanes's theory of Physiological Selection—which assumes sterility or infertility between first crosses as the fundamental fact in the origin of species—does not accord with the general phenomena of hybridism in nature." In the first place, as shown above, "infertility between the first crosses" is by no means out of accord with "the general phenomena of hybridism in nature"—seeing that all degrees of such infertility, from the slightest perceptible amount of prepotency up to absolute sterility, are of the most general occurrence in nature. In the second place, why Mr. Wallace should suppose that in my view physiological selection can only act as regards first crosses, and not also as regards hybrid progeny, I have no means of surmising.

the whole of Mr. Wallace's criticism (even as regards Birds and Mammals) goes upon the supposition that Mr. Gulick and I believe that, if physiological selection ever acts in any case *at all*, it must necessarily act *alone*. For reasons afterwards to be given, I do indeed believe that in some cases it may act alone (in this differing from Mr. Gulick); but, clearly, whether or not there are any such cases, is a question quite distinct from that touching the validity of a criticism which attributes to our theory the absurd dogma, that segregate breeding which arises from physiological isolation, can never be associated with segregate breeding that may arise from any other form of isolation. And that the whole of Mr. Wallace's criticism collapses when once this correction has been supplied, is proved most effectually by the curious fact that, *after having himself supplied the correction, he reproduces our theory as an original one of his own.* How he can have supposed that I did not entertain the possibility of physiological selection being associated with natural selection, "psychological selection," or any other known form of isolation (excepting only the geographical), I am quite at a loss to understand; seeing that from end to end of my paper I continually refer to such association—especially as regards natural selection. And, if possible, I am still less able to understand Mr. Wallace's carelessness in this connection with reference to Mr. Gulick's paper; because there the belief is repeatedly and most clearly expressed, that without such association, "segregate fecundity" *can never act at all*—which is precisely the theory which Mr. Wallace proceeds to elaborate on his own account.

It is now time to show, by means of quotations, how unequivocal and complete is Mr. Wallace's adoption of our theory:

"The simplest case to consider will be that in which two forms or varieties of a species, occupying an extensive area, are in process of adaptation to somewhat different modes of life within the same area. If these two forms freely intercross with each other, and produce mongrel offspring which are quite fertile *inter se*, then the further differentiation of the forms into two distinct species will be retarded, or perhaps entirely prevented; for the offspring of the crossed unions will be, perhaps, more vigorous on account of the cross, although less perfectly adapted to the conditions of existence than either of the pure breeds; and this would certainly establish a powerful antagonistic influence to the further differentiation of the two forms.

Now, let us suppose that a partial sterility of the hybrids between the two forms arises, in correllation with the different modes of life and the slight external or internal peculiarities that exist between them, both of which we have seen to be real causes of infertility. The result will be that, even if the hybrids between the two forms are still freely produced, these hybrids will not themselves increase so rapidly as the two pure forms; and as these latter are, by the terms of the problem, better suited to their conditions of life than are the hybrids between them, they will not only increase more rapidly, but will also tend to supplant the hybrids altogether whenever the struggle for existence becomes exceptionally severe. Thus, the more complete the sterility of the hybrids the more rapidly will they die out and leave the two parent forms pure. Hence it will follow that, *if there is greater infertility be ween the two forms in one part of the area than the other, these forms will be kept more pure wherever this greater infertility prevails*, will therefore have an advantage at each recurring period of severe struggle for existence, and will thus ultimately supplant the less infertile or completely fertile forms that may exist in other portions of the area. It thus appears that, in such a case as here supposed, natural selection would preserve those portions of the two breeds which were most infertile with each other, or whose hybrid offspring were most infertile; and would, therefore, if variations in fertility continued to arise, tend to increase that infertility. It must particularly be noted that this effect would result, not by the preservation of the infertile variations on account of their infertility, but by the inferiority of the hybrid offspring, both as being fewer in numbers, less able to continue their race, and less adapted to the conditions of existence than either of the pure forms. It is this inferiority of the hybrid offspring that is the essential point; and as the number of these hybrids will be permanently less where the infertility is greatest, therefore those portions of the two forms in which infertility is greatest will have the advantage, and will ultimately survive in the struggle for existence."

We have here a full acceptance of the theory of physiological selection. For it is represented, as Mr. Gulick and I have represented, that, if "two forms or varieties" occupying a common area are to undergo further differentiation at the hands of natural selection, it becomes a highly favoring condition to the process that some degree of segregate fecundity should arise (if it has not already arisen) between these two forms or varieties; seeing that "if these two forms freely intercross with each other, and produce mongrel offspring which are quite fertile *inter se*, then the further differentiation of the forms into two distinct species will be retarded, or perhaps entirely prevented." Here the importance of segregate fecundity, or physiological selection, as a factor in the differentiation of specific types on common areas is *fully recognised;* and the *only* respect in which Mr. Wallace alleges that his view of the matter differs from the view of Mr. Gulick and myself, is in drawing special attention to the part which is played by the infertility, or other "inferiority," of the mongrels. But clearly, this infertility, or other inferiority, of the mongrels, in all cases where it occurs, *is part and parcel of the segregate fecundity of the parent forms.* Whether the segregate fecundity has reference to first cros ses alone, or likewise to second crosses, it is segregate fecundity all the same; and the only difference is that for the same degree of segregate fecundity in first crosses, the process of physiological selection will become the more effective in proportion to the degree in which the infertility extends also to second crosses. But I think it is very doubtful whether such infertility (or inferiority) on the part of mongrels can react upon the sexual system of their parent forms, so as directly to increase whatever degree of segregate fecundity may have already arisen between these forms. Does the high sterility of mules ana mutes, for instance, tend to diminish the degree of fertility that obtains between horses and asses? The only way in which even an absolute degree of sterility (or other inferiority) on the part of mongrels or hybrids may clearly be seen to operate in this direction, is as a negative condition; not as an active cause. In the proportion that mongrels are impotent with one another, they will not so much compete with their parent forms for food, etc.; and in the proportion that they are impotent with their parent forms, they will not counteract any tendency which the latter may continue to develop in the direction of a still further segregation. If the mongrels are fully vigorous and fully fertile, both *inter se* and with their parent forms, the effect will be to retard, if not altogether to prevent, any further progress ot physiological separation between the parent forms; because the free intercrossing of the mongrels with one another, and also with their parent forms, will be continually supplying progeny in which the physiological peculiarity is either attenuated or altogether abolished. But this is quite a different thing from supposing that infertility (or inferiority) of the mongrels can react upon the generative system of the parent forms, so as to increase in them the physiological peculiarity on which their segregate breeding depends: infertility (or inferiority) of the mongrels is but a negative condition which favors the preservation of further degrees of this segregate breeding, if such further degrees should be induced by any other causes.

Now, it does not appear that Mr. Wallace has clearly perceived this important distinction, because he throughout speaks of "this inferiority of the hybrid offspring as the essential point." Obviously, however, the essential point is the physiological variation in the parent forms, i. e., the original occurrence and subsequent development of infertility between the first crosses. Granting to Mr. Wallace, for the sake of argument, that this development could not proceed at all, were it not for the inferiority of the mongrels; still the inferiority of the mongrels need not be the cause of this development. Therefore it is most incorrect to say, "it must be particularly noted that this effect (i. e., increase of infertility between the parent forms) would result, not by the preservation of the infertile variations on account of their infertility, but by the inferiority of the hybrid offspring." "This effect" must be due to causes which act upon the generative systems of the parent forms, even though such causes might be *counteracted* by the *withdrawal* of the negative condition in question.

I trust, then, it has now been rendered sufficiently clear that, no matter how infertile the hybrid progeny may become, and no matter at how great a disadvantage they may thus (or otherwise) be placed in their struggle for existence with the parent varieties, it is not apparent that their infertility (or their extinction) can ever become the cause of a further increase of infertility arising between their parent forms. Consequently, although this is the cause assigned by Mr. Wallace, when he comes to "the essential point" of showing how it is to act so as to increase cross-sterility between the parent forms, he naïvely substitutes the sentence which I have printed in italics—which assumes a "greater infertility between the two forms" as arising through any other causes that we may choose to suppose. The very thing that his entire argument professes to explain (i. e., the rise and development of cross-sterility between the parent varieties) is slipped in as granted, or given by other causes than those which are said to explain it.*

Having thus endeavored to make it as clear as I can, that the causes of segregate fecundity, both in its origin and subsequent "increase," must be causes acting on the physiology of the segregating forms themselves, and not the effects of these causes in the character of their mongrel offspring; I must next comment upon the extraordinary idea which underlies the whole of Mr. Wallace's exposition, and which in one place he expressly states. This extraordinary idea is that the theory of physiological selection, as held both by Mr. Gulick and myself, takes no cognizance of the possible effects of cross-sterility in leading to infertility or inferiority on the

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* The only conceivable way in which infertility (or other inferiority, of hybrids could react on the sexual system of their parent forms, is one which Mr. Wallace appears to have missed: at all events he has nowhere stated it. This way is as follows. Suppose A and B to be two varieties which produce comparatively infertile hybrids. In the proportion that the hybrids are infertile, or otherwise inferior, it must be a disadvantage to both varieties for individuals belonging to one to cross with individuals belonging to the other, because by so doing they are wasting their time and their energy in propagating comparatively poor offspring—thereby failing to impress their characters on the next generation as effectually as they might have done by pairing homogamously. Hence, those individuals which do pair homogamously will leave a larger number—or better quality—of offspring to the next generation, than is left by those which fail to pair homogamously. Hence, also, in the course of many generations a selective premium will be set on the homogamous pairing, A plus A, B plus B, whether such pairing be due to a sexual instinct or to a sexual incompatibility. For example, if horses and asses were to occupy the same area for a sufficient length of time, it is conceivable that the instinct which many horses now present of preferring asses to their own kind would become obsolete; because the horses or mares which have such an instinct would always fail to leave progeny that could transmit it, while such would not be the case with the horses and mares which preferred to pair homogamously, and so it might be if a physiological instead of a psychological character were concerned. But now observe, if this consideration were adduced, I should not be concerned to dispute it. For, even if such a principle of segregation does obtain, to what category does the principle belong? Clearly it does not belong to natural selection, inasmuch as a mere failure to impress individual characters on the next generation is not a matter of life and death in the struggle for existence. But, no less clearly, it does belong to physiological selection; and therefore, if it be an active principle in nature, it is an additional cause of segregate fecundity in first crosses. Moreover, such a principle, if it ever acts, presupposes some considerable degree of sexual differentiation as already given by some other cause.

part of mongrel progeny. I call this an extraordinary idea, because it appears to me most extraordinary that Mr. Wallace can have read our papers, and then have supposed that he was adding anything to our theory by arguing the points which he does argue in the above quotation. When once this argument is correctly stated, it amounts, as we have just seen, to nothing more than pointing out how a segregate fecundity of first crosses will have a better chance of increasing, if the mongrel progeny are infertile or inferior. But surely this goes without saying; or, if it be said, let it be added that physiological selection, when it thus extends to second crosses, is really or ultimately due to physiological selection as regards the first crosses. If the segregate fecundity of the first crosses is of such a kind, that, besides tending to a physiological isolation of the parent forms, it leads to inferiority of the mongrel progeny; this is merely a further expression of the segregate fecundity in question. Its effect is that of so far extinguishing the influence of progeny in the subsequent history of parental segregation: therefore, its effect is just the same as if, owing to a somewhat higher degree of segregate fertility in the first instance (i. e., in the first crosses), a proportionately smaller number of mongrel offspring had been produced at all. In either case the result (physiological differentiation) is equally due to causes acting on the sexual system of the parent forms; and whether this effect is brought about by a suppression of progeny as to their numbers alone, or likewise as to their efficiency, is quite immaterial to the theory of physiological selection. Which shows once more how wide of the mark is Mr. Wallace's statement, that "the inferiority of the hybrid offspring is the essential point" in any process of sexual segregation. The "essential point" must always be the original occurrence and subsequent "preservation of the infertile variations" arising between the parent forms, whether these variations are only in the direction of producing a smaller number of mongrels, or also in that of suppressing their efficiency when produced.

Upon the whole, then, it is surely the oddest of misconceptions on Mr. Wallace's part that has led him to present the above-quoted "argument" as a substitute for the theory of physiological selection. As far as it goes, and as far as it is sound, it is the theory of physiological selection pure and simple—neither adding to, nor detracting from it one iota. Nevertheless, the "argument" has not yet gone far enough to embody some of the other elements of the theory. Therefore I will now continue the quotation :

"The differentiation of the two forms into distinct species, with the increase of infertility between them, would be greatly assisted by two other important factors in the problem. It has already been shown that, with each modification of form and habits, and especially with modifications of color, there arises a disinclination of the two forms to pair together ; and this would produce an amount of isolation which would greatly assist the specialisation of the forms in adaptation to their different conditions of life. Again, evidence has been adduced that change of conditions or of mode of life is a potent cause of disturbance of the reproductive system, and, consequently, of infertility. We may therefore assume that, as the two forms adopted more and more different modes of life, and perhaps acquired also decided peculiarities of form and coloration, the infertility between them would increase or become more general ; and as we have seen that every such increase of infertility would give that portion of the species in which it arose an advantage over the remaining portions in which the two varieties were more fertile together, all this induced infertility would maintain itself, and still further increase the general infertility between the two forms of the species."

Here we perceive that Mr. Wallace, after having adopted the theory of physiological selection in its main elements, next proceeds to supplement that theory (as Mr. Gulick and myself had previously done), by showing how greatly the principle of physiological selection must be assisted by any association with other forms of isolation, or segregate breeding. The only difference between Mr. Wallace and ourselves here is, that while he instances but three or four forms of segregate breeding (or homogamy) with which physiological selection may be associated, I had previously considered several others in addition to these, while Mr. Gulick had gone into the matter still more exhaustively. Therefore, here as elsewhere, I can only account for the character of Mr. Wallace's criticism by supposing that he read our papers inattentively in the first instance, and was afterwards influenced by "unconscious memory" in his subsequent cogitations upon the problem of cross-sterility.

And now, finally, in order to show this still more completely, I may quote the whole paragraph which concludes his long discussion of that problem:

The preceding argument, it will be seen, depends entirely upon the assumption that some amount of infertility characterises the distinct varieties which are in process of differentiation into species; and it may be objected that of such infertility there is no proof. This is admitted; but it is urged that facts have been adduced which render such infertility probable, at least in some cases, and this is all that is required. It is by no means necessary that all varieties should exhibit incipient infertility, but only some varieties; for we know that, of the innumerable varieties that occur, but few become developed into distinct species; and it may be that the absence of infertility, to obviate the effects of intercrossing, is one of the usual causes of their failure. All I have attempted to show is, that when incipient infertility does occur in correlation with other varietal differences, that infertility can be, and in fact must be, increased by natural selection; and this, it appears to me, is a decided step in advance in the solution of the problem."

This serves to convey a very accurate summary of the whole "preceding argument"; and it is likewise an admirably concise restatement of the theory of physiological selection. The only points in it to which I object—considered as an epitome of my own paper—are as follows. First, Mr. Wallace has not proved quite so good an advocate as he might have proved, had he looked more closely into the evidence "that some amount of infertility characterises the distinct varieties which are in process of differentiation into species." For although he says, properly enough, that his "preceding argument"— i. e., the theory of physiological selection—"depends entirely upon the assumption" that such infertility does "characterise distinct varieties which are in process of differentiation into species"; still he is wrong in saying it is "admitted" that in favor of this assumption there is "no proof" beyond what he has himself "urged" in the way of "facts which render such infertility probable": there are many other facts which not only render such infertility probable, but prove it to be actual. Secondly, although I quite agree with Mr. Wallace in holding that natural selection must often, as I said in my original paper, "co-operate" with physiological selection, still I must point out that the particular form of segregate breeding to which he here alludes is not natural selection at all; but (as explained in the foot-note to page 15) physiological selection pure and simple.

My objections, however, with regard to these two points have no reference to the validity of Mr. Wallace's restatement of my views; and the fact that this restatement has been given with the most incomprehensible unconsciousness that it is a restatement, does not appear to me to detract from the significance of the argumentative suicide in which his entire criticism is thus found to terminate.*

With the self-destruction of this criticism I am left without any other to answer; and I should not have occupied so much space in dealing with this one, were it not that the high estimation in which Mr. Wallace is so deservedly held by all other naturalists is calculated to render almost incredible the peculiar position to which he has eventually gravitated with reference to my views—professing hostility on the one hand, while reproducing them as original on the other. The misunderstanding of my ideas which this state of matters represents, might have led me to wonder whether I could

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*I am the more surprised that Mr. Wallace did not perceive his almost complete adoption of my views in this latest publication of his own, because I had previously had occasion to point out a partial adoption of them in an earlier publication of his on the same subject. The following is what I said upon that occasion—viz., in the *Nineteenth Century*, January, 1888:

"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, etc.; 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, etc., 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."

Now, in his *Darwinism*, Mr. Wallace again reproduces this instance of "physiological selection," without even yet appearing to perceive that both in my original paper upon the subject and in my answer to his criticism as above quoted, I adduce this particular instance of physiological selection as a typical one. Therefore, when he now says:—"Another mode of isolation is brought about by the variety—either owing to habits, climate, or constitutional change—breeding at a slightly different time from the parent species: this is known to produce complete isolation in the case of many varieties of plants": he is merely restating what I have repeatedly given as an unquestionable case of physiological selection.

possibly have rendered my meaning more clear in the first instance, were it not that this misunderstanding extends in an even greater measure to Mr. Gulick's paper than it does to mine. For seeing that the whole criticism is founded on the erroneous idea that our theory supposes physiological selection always to act alone, the misconception becomes positively ludicrous in its relation to Mr. Gulick's views; seeing that, as previously stated, Mr. Gulick not only agrees with me in holding that physiological selection must be greatly fortified by being associated with any other form of homogamy, but even goes so far as to agree with Mr. Wallace that, unless it is so fortified, it can never act at all. So that, as far as physiological selection is concerned, Mr. Gulick's theory is precisely identical with that of Mr. Wallace, and differs from his statement of it only in recognising a number of forms of homogamy, in addition to natural selection, sexual selection, etc., with which the principle of physiological selection may be associated.

George J. Romanes.