ART. LV.—*The Preservation and Accumulation of Cross-infertility*; by JOHN T. GULICK.

IN his work on "Darwinism" in a section entitled "The Influence of Natural Selection upon Sterility and Fertility," Mr. Wallace reaches the conclusion that "If it [the cross-infertility] was so closely correlated with physical variations or diverse modes of life as to affect, even in a small degree, a considerable proportion of the individuals of the two forms in definite areas, it would be preserved by natural selection." (p. 178). That the infertility of an incipient species with its nearest allies is often preserved and accumulated, no one can doubt; but there are, it seems to me, very strong reasons for believing that this can never be due to natural selection. Natural selection is the *exclusive* breeding of those best adapted to the environment of the species, through the failure to propagate of those that are less adapted; and the *separate* breeding of those that are equally adapted introduces a wholly different principle. In order to produce the cumulative modification of a variety, selection, whether natural or artificial, must preserve certain forms of an intergenerating stock to the exclusion of other forms of the *same* stock. I may select bantams as the object of my attention for a few years, and then excluding them, raise only Shanghai fowls; but this is not the form of selection by which these divergent races were produced. Again, if rats should supplant mice in any country, some persons might call it natural selection, but such natural selection would modify neither rats nor mice. On the other hand if certain variations of mice are better able than the rest to escape their pursuers, they will leave the most numerous offspring, and modification of species will commence. Now if we turn to page 175 of Mr. Wallace's book, we find, that in

the illustrative case introduced by him, the commencement of the cross-infertility is in the relations to each other of two portions of the species partially segregated from the rest by occupying a definite part of the general area, and partially segregated from each other by different modes of life. These two physiologically segregated local varieties, being, by the terms of his supposition, better adapted to the environment than the more freely interbreeding forms in the other parts of the general area, increase till they supplant these original forms. Then, in some limited portion of the general area, there arise two still more divergent varieties, with greater mutual infertility, and therefore with still less commingling of the two, and with power to prevail throughout the whole area.*

The process here described, if it takes place, is not modification by natural selection, but a supplanting which does not produce modification, and which does not take place till a new and complicated adjustment has arisen in a portion of the species that is partially segregated, by occupying a definite portion of the area. This new adjustment introduces two new varieties, each with unabated fertility with the other variety; and the process, or principle, by which it is reached receives no explanation in the section we are now considering; but from what he says on page 184, we may judge that his only explanation is an application of the principle of Intensive Segregation, more especially that form of this principle which I have described as the effect of isolation on unstable adjustments, but which Mr. Wallace has rejected as untenable. Moreover, in the supposed case pictured by Mr. Wallace, the principle, by which the two forms are kept from crossing and are preserved as permanently distinct forms, is no other than that which Mr. Romanes and myself have discussed under the terms *Physiological Selection* and *Segregate Fecundity*. Not only is Mr. Wallace's exposition of the divergence and the continuance of the same in accord with these principles which he has elsewhere rejected, but his whole exposition is at variance with his own principle, which, in the previous chapter, he vigorously maintains in opposition to my statement that many varieties and species of Sandwich Island land molluscs have arisen while exposed to the same environment in the isolated groves of the successive valleys of the same mountain range. If he adhered to his own theory "The greater infertility between the two forms in one portion of the area"

* This brief outline of the method by which Mr. Wallace thinks cross-infertility has been produced and accumulated, though given in another connection, in my article on *Utilitarianism as the Exclusive Theory of Organic Evolution* (this Journal, July, 1890), is here repeated, that the correspondences and divergences in the different theories we are here discussing may be better apprehended.

would be attributed to a difference between the environment presented in that portion and that presented in the other portions; and the difficulty would be to consistently show how this greater infertility could continue unabated when the varieties thus characterized spread beyond the environment on which the character depends. But, without power to continue, the process which he describes would not take place. In order to solve the problem of the origin and increase of infertility between species he gives up his own theory and adopts not only the theory of Physiological Selection but that of Intensive Segregation through Isolation, though he still insists on calling the process natural selection; for on page 183 he says, "No form of infertility or sterility between the individuals of a species can be increased by natural selection unless correlated with some useful variation, while all infertility not so correlated has a constant tendency to effect its own elimination." Even this claim he seems to unwittingly abandon when on page 184 he says: "The moment it [a species] becomes separated either by geographical or selective isolation, or by diversity of station or of habits, then, while each portion must be kept fertile *inter se*, there is nothing to prevent infertility arising between the two separated portions."

Mr. Wallace adopts these two fundamental doctrines of the theory of Divergent Evolution through Segregation, but he does not apply them exactly as I would. Why, for example, should he resort to the supposition that when the two divergent varieties occupying the extensive area are everywhere somewhat infertile with each other the increase of that character is gained *only in a limited portion of the area*, and then spreads by conquest? Would it not be simpler, and at the same time truer to the facts of nature, to assume, that the divergent variety can not arise except as it is aided by some form of positive segregation, preventing free crossing with the parent stock; and that in cases where this prevention is only partial, any cross-infertility once introduced will diminish the swamping effect of the crossing that occurs, and will *everywhere* tend to increase, because the majority of each generation of the pure form will be the descendants of those whose cross-infertility was above the average. There are, moreover, other forms of negative segregation equally effective with cross-infertility and Segregate Fecundity. It often occurs that when segregation with divergence has once begun to show itself, the variations that are most fully endowed with the new character, (though less adapted to the new mode of life than the old form is to the old mode of life) will best escape both the severe competition with the rest of the species and the swamping effect of crossing. In time the pressure for food becomes as

great with the new form as with the old, and escape from competition ceases. Under these circumstances either the maladaptation or the infertility of the hybrids will be of the highest importance in preventing swamping. But, is it necessary to suppose, as Mr. Wallace does, that the infertility will disappear in cases where the hybrids are as well adapted as the pure forms? In such cases, during the preliminary period when escape from competition is gained most fully by those most fully segregated, there will naturally be a rapid accumulation of all segregative endowments; but, when that condition ceases, there will still be a sufficient reason for the continuance, or even increase, of the cross-infertility in the fact that more than half of each generation of the pure form will be the descendants of those whose cross-infertility and other segregative endowments are above the average. This principle is one form of what I have called *Self-Cumulative Segregation*.

This law of self-accumulation does not seem to apply to cross-infertility (or to any other form of negative segregation) that is not associated with positive segregation. Nor is it quite clear that, when unassociated with negative segregation it applies to positively segregating characters (such as social and industrial instincts that lead animals of one kind to pair together, and the prepotency of the pollen of a given kind on the stigma of the same kind securing a similar result for plants). When, however, characters producing positive but incomplete segregation are associated with those producing negative segregation, both classes of characters must tend to increase till the segregation becomes pronounced. As soon as this point is reached, the *Reflex Selection*, by which the different portions of the species have been kept in harmonious relations with each other, is suspended, and there is nothing but the force of heredity to hold them in correspondence; but the force of heredity, securing this correspondence, has itself been created by the long continued *Reflex Selection*, and when this is removed, it gradually fails, and divergences of all kinds multiply, increasing the incompatibility of the two forms. Thus arises diversity of habits, diversity of sexual and social instincts, and diversity in the affinities of the male and female elements; and in each respect this diversity tends toward the point of complete incompatibility.

Positive segregation diminishes the amount of crossing, and negative segregation diminishes the swamping effect of crossing when it occurs. Negative segregation may be of the following forms: (1) lack of fertility of first crosses and of the hybrids, which I call *Segregate Fecundity*; (2) lack of *Vigor* in hybrids, which I call *Segregate Vigor*; (3) lack of adapta-

tion in hybrids, which I call Segregate Adaptation; (4) lack of escape from competition in hybrids, as compared with pure forms, which I call Segregate Escape from Competition. Of these all but the 4th were considered in my paper on "Divergent Evolution through Cumulative Segregation," where I endeavored to show that in their coöperation with positive segregation they were parallel factors producing similar results. Now in his supposed case (pp. 173-9), Mr. Wallace has treated the Segregate Adaptation, or hybrid maladaptation, as if it were the effective factor by which the hybrid infertility is alone enabled to increase or even continue. I see no reason why this should be so. The effectiveness of these negative factors in preserving a species must depend on their being associated with positive segregation; but the effectiveness of any one of the negative factors is not destroyed by the absence of the others; though Segregate Escape from competition is, under ordinary conditions, confined to the preliminary stages of divergence; and may, in certain cases, be the necessary condition leading to the other forms of negative segregation.

Mr. Wallace's criticism of the theory of physiological Selection (pp. 180-3) is unsatisfactory; (1) because he has adopted the fundamental principle of that theory, on pages 173-9, in that he maintains that without the cross-infertility the incipient species there considered would be swamped; (2) because he assumes that physiological selection pertains simply to the infertility of first crosses, and has nothing to do with the infertility of mongrels and hybrids; (3) because he assumes that infertility between first crosses is of rare occurrence between the species of the same genus, ignoring the fact that, in many species of plants the pollen of the species is prepotent on the stigma of the same species when it has to compete with the pollen of other species of the same genus; (4) because he not only controverts Mr. Romanes' statement that cross-infertility often affects "a whole race or strain," but he gratuitously assumes that the theory of Physiological Selection excludes this "racial incompatibility" which Mr. Romanes maintains is the more probable form, and bases his computation on the assumption that the cross-infertility is not associated with any form of positive segregation; (5) because he claims to show that "all infertility not correlated with some useful variation has a constant tendency to effect its own elimination, while his computation only shows that, if the cross-infertility is not associated with some form of positive segregation, it will disappear; and (6) because he does not observe that the positive segregation may be secured by the very form of the physiological incompatibility. Many species of plants may be promiscuously distributed over the same area, and still be com-

pletely segregated by what I have called Potential Segregation. In other words, if the pollen of each species is potent only when falling on the stigma of the same species then the species are completely segregated though growing in the same area. Still further two species may be fairly fertile when artificially crossed, and yet be completely segregated while growing together, through the fact that the pollen of either species when falling on its own stigma will be prepotent over the pollen of the other species even though the alien pollen has fallen upon the stigma considerable earlier. This I have called Prepotential Segregation. Now a variety that is segregated from the parent form by prepotential Segregation and cross-infertility, will neither fail of propagating nor be swamped by crossing though it is indiscriminately mingled with the parent form. In my paper on "Divergent Evolution" I have referred to this special combination of positive and negative segregation, produced by the incompatibility of the male and female elements, and have endeavored to show that when these characters occur together, they tend to increase in intensity according to a law of self-accumulation. (Linn. Soc. Jour. Zool., vol. xx, pp. 239-40, 259-60). Without here entering into any computation, it is evident that the prepotency of the pollen of each kind with its own kind, if only very slight, will prevent cross-fertilization as effectually as a moderate degree of instinctive preference in the case of an animal, and if segregate fecundity, (i. e. cross-infertility) is added it will tend to keep the variety from the swamping effect of the little crossing that occurs, and the variations that are above the average in these characters will have the largest influence on the pure form in each successive generation.

I regard Physiological Segregation as including all kinds of incompatibility between the male and female elements of different groups, whether these groups are varieties of one species, or species of one genus, or species of different genera, or species representing still more divergent groups; and I maintain that the importance of this principle in the origin and continuance of divergent groups, cannot be exaggerated in the case of organisms whose fertilizing elements are freely distributed by wind or water; for in these cases the segregate compatibility and cross incompatibility of the male and female elements may be the means by which the prevention of free crossing is secured, as well as the means by which the swamping effect of the crossing that occurs is prevented. There is, it seems to me, strong reason to believe that this principle is a leading factor in the segregation of multitudes of water animals, as well as in the segregation of species of plants, whether terrestrial or aquatic; and Mr. Romanes has rightly emphasized the importance of investigations in this line.

26 Concession, Osaka, Japan.