Unstable Adjustments as affected by Isolation.

In a brief passage in his very suggestive volume on "Darwinism," Mr. Wallace refers to a principle which seems to me to be worthy of much wider application than he has given. It is a key which requires only a little filing to prepare it for unlocking some difficult problems in divergent evolution. Speaking of the infertility of crosses, he says:—"It appears as if
fertility depended on such delicate adjustment of the male and female elements to each other that, unless constantly kept up by the preservation of the most fertile individuals, sterility is always ready to arise. So long as a species remains undivided, and in occupation of a continuous area, its fertility is kept up by natural selection; but the moment it becomes separated, either by geographical or selective isolation, or by diversity of station or habits, then, while each portion must be kept fertile in a separate portion, there is nothing to prevent infertility arising between the two separated portions (p. 184). Here is an application of the principle of segregation, or of like to like in groups that do not cross, in which indiscriminate separation is followed by increasing divergence in the different portions, not because they are exposed to different conditions or environments. But because they have the advantage in such divergence, not because there is any need that the function should be performed more perfectly in one portion than in the other, but because intergeneration, which is the principle by which correspondence of function is secured, has been suspended for some generations; and, in the absence of intergeneration, neither natural selection nor any other principle is capable of preserving complete correspondence. In organisms that reproduce sexually, the causes of divergence are many, though they may all be classed as causes of segmentation, while the causes of correspondence with variation, whether of functions or of structures, are causes of intergeneration between partial segregations. If the environments surrounding the isolated portions are different, and the different forms of natural selection, may become divergent; if the use continues unchanged, some useless divergence in the method of securing the use may appear. Or, if all the relations to the environment, whether useful or useless, remain unchanged, the adjustment of the male and female elements to each other are liable to become slightly divergent, producing mutual infertility. Or, when the forms are arranged in a state of mutual infertility, color in their mates may become slightly different. Through some slight difference in the hereditary elements, distributed in each separated portion at the first, one or all of these causes of accumulated divergence may be introduced. I think it is evident that we have here a general principle, which is applicable to a wide range of divergences as it is to the divergence that produces mutual infertility in such adjustments.

The context shows that the prominent idea in Mr. Wallace's mind was divergence in the adjustment of the male and female elements through correlation with some diversity of form or color, resulting from divergent forms of natural selection, that had been induced by exposure to somewhat different conditions and restricted to different environments, where it has now been quoted, it gives an explanation of similar divergences when the separated portions are exposed to the same environment, and to such as are possible to be gained by divergence. This is one of the principles I have used in the explanation of the divergences of Sandwich Island land mollusks; and I think that in the earlier stages of the development of infertility between allied forms, it is the only explanation that is applicable. It should, however, be remembered that, for divergence of this kind, it is not always necessary that the isolation should be either complete or very long continued, and that, when the forms that are not fully fertile with each other meet and more or less commingle, there is not the necessity of those very laws of propagation, without any aid from natural selection, a constant increase in the ratio of the pure breeds to the mongrels, and an accumulating intensity in the segregative instincts and the physiological incompleteness. As this point has been fully discussed in my paper on "Divergent Evolution," I do not need to enlarge on it here (see Linn. Soc. Journ., Zoology, vol. xx. pp. 248-72).

There is, however, another phase of the subject which is indicated by Mr. Wallace's suggestion that infertility depends on such a delicate adjustment that it is more easily affected by isolation than other adjustments. This is, I think, a very interesting point, as it suggests how it is that, in some cases at least, physiological divergence of this kind is one of the first phases of divergence that arises. But in some species such adjustments seem to be more delicate than this, and therefore more easily disturbed; while in others, several sets of adjustments, as colours and other recognition marks, with the preferences that correspond, and the habits of feeding and defence are in a state of equilibrium, the stability or instability of which is about the same as of that which determines the relations of the male and female elements. In this last class of cases, several forms of divergence may arise during the same stage of development, and that too when the isolated portions are exposed to the same environment. In some species a large number of characters are in a state of unstable adjustment. As Prof. Lankester has suggested near the close of his review of Mr. Wallace's book, this cause of divergence seems to be specially operative in the case of human faculties. But variability with plasticity of type is not the only condition that affects the stability of segregated portions of a species. Other things being equal, a single pair of any species is much less likely to represent the average of all the characters of the species than a million pairs. This consideration throws light on the comparative lack of divergence between the land animals of England and those of Ireland, which lack has been referred to by Mr. Wallace as an objection to my theory. In this case, many millions of some of the species were probably existing in each district at the time of the separation. As Prof. Lankester has pointed out, the representatives of the human species in the two districts have somewhat diverged; and the probability is, that if we were equally acquainted with the other species, we should find other examples of divergence in minor points. If the isolation is made more complete, and is longer continued, I believe the divergence will gradually become more apparent.

Mr. Wallace has mentioned another class of divergences which are best explained by the principle we are now considering—as he seems to have apprehended, though the process is not stated here as clearly as when discussing the divergences that produce infertility. The passage is as follows:—"The enormously lengthened plumes of the bird of paradise and of the peacock must be rather injurious than beneficial in the birds' ordinary life. The fact that they have been developed to so great an extent in a few species is an indication of such perfect adaptation to the conditions of existence, such complete success in the battle of life, that there is, in the adult male at all events, a surplus of strength, vitality, and growth-power which is able to expend itself in this way without injury. That such is the case is shown by the great abundance of most of the species which possess these wonderful superfluities of plumage. Why, in allied species, the development of accessory plumes has taken different forms, we are unable to say, except that it may be due to that individual variability, which has served as the starting-point for so much that seems to us strange in form, or fantastic in colour, both in the animal and vegetable world" ("Darwinism," p. 293. The italics are mine).

It is no small gratification to me that Mr. Wallace has found this principle of unstable adjustment worthy of application to two important classes of divergences; and that, in the ease of one of these classes, he has recognized that correspondence in such adjustments cannot be continuously maintained between the isolated portions of a species. I, moreover, have some hope that, when he understands the relation in which instability and isolation stand to each other in my theory, he will admit that it throws some light on the remarkable divergences of Sandwich Island land mollusks. The subject was only incidentally touched upon in my paper on "Divergent Evolution through Cumulative Segregation," but will be more fully discussed in a supplemental paper on "Intensive Segregation."