

ART. III.—*Divergent Evolution and the Darwinian Theory*;
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IN a paper on *Divergent Evolution through Cumulative Segregation* (Linnean Soc. Journal, Zoology, vol xx, pp. 189–274), I have endeavored to show that selection, whether natural or artificial, is a process that has no tendency to produce divergent evolution, unless different sections of one original stock are subjected to different forms of selection, while at the same time some cause prevents free crossing between the different sections. We now inquire whether Darwin has made us acquainted with any cause or combination of causes that, without the aid of man, produces diversity of selection and at the same time the independent generation of the different classes of variations thus preserved.

Darwin discusses the causes of natural selection more fully than the causes of diversity of natural selection. He does not

speak of uniformity and diversity of natural selection, but of the individuals of the same species living under the same external conditions as being modified in the same way, and of those living under dissimilar external conditions as being modified in different ways. Again, he speaks of "the divergent tendency of natural selection," resulting from "the principle of benefit being derived from divergence of character," as explaining divergence of character in the members of one species competing with each other on a common area. How the contradictions in the two statements are to be reconciled, and how, in the second case, the unifying influence of free-crossing is prevented, he does not show, so far as I can discover. As the subject is of the highest importance in the explanation of divergent evolution, and as it is specially desirable to get as clear an understanding as possible of Darwin's method of explanation, I shall consider his reasoning somewhat fully.

Some degree of Local Separation under Different Environments.

Darwin often speaks of the influence of crossing in retarding or preventing the formation of new races and species: but, from the following extracts from his *Origin of Species*, it will be seen that it is not quite so clear what combination of causes he considered necessary for the production of two or more species from one original species. The obscurity in his statements results, I think, from the fact that "a new species" may be one that has been formed by monotypic transformation, the old form disappearing with the production of the new, or it may be one that has arisen through polytypic transformation which is the modification of one branch of the species, while other branches remain either unmodified or modified in other ways. For the formation of a new species, in the former meaning of the word, he evidently did not consider it necessary that the species or any part of it should enter a new environment, or that crossing should be prevented. But did he not consider both these conditions necessary for the formation of two or more species from one original species?

He says "Intercrossing will affect those animals most which unite for each birth and wander much, and which do not breed at a very quick rate. Hence with animals of this nature, for instance birds, varieties will generally be confined to different countries; and this I find to be the case. With hermaphrodite organisms which cross only occasionally, and likewise with animals which unite for each birth, but which wander little and can increase at a very rapid rate, *a new and improved variety might be quickly formed on any one spot*, and might there maintain itself in a body and afterward spread, so that

the crossing would be chiefly between *the individuals of the new variety living together in the same place. . . .*

"Even in the case of animals which breed slowly and unite for each birth, we must not assume that *the effects of natural selection* will always be immediately overpowered by free intercrossing; for I can bring a considerable body of facts showing that within the same area, varieties of the same animal *may long remain distinct*, from haunting different stations, from breeding at slightly different seasons, or from varieties of the same kind preferring to pair together. . . .

"Isolation, also, is an important element in the changes effected through natural selection. *In a confined or isolated area, if not very large, the organic and inorganic conditions of life will be almost uniform: so that natural selection will tend to modify all the varying individuals of the same species in the same manner.* Intercrossing with the inhabitants of the surrounding districts will, also, be prevented. Moritz Wagner has lately published an interesting essay on this subject, and has shown that the service rendered by isolation in preventing crosses between newly formed varieties is probably greater even than I have supposed. But from reasons already assigned, I can by no means agree with this naturalist that migration and isolation are necessary for the formation of new species." [Origin of Species, fifth edition,* Chapter IV, Section on "Circumstances favorable for the production of new forms through Natural Selection."]

Again in the same chapter, in the section on "Various Objections," in answer to the question, "How, on the principle of natural selection, can a variety live side by side with the parent-species?" he replies, "If both have become fitted for slightly different habits of life or conditions, they might live together, though in the case of animals which freely cross and wander much about, *varieties seem to be almost always confined to distinct localities.* But if we put on one side polymorphic species, in which the variability seems to be of a peculiar nature, and all mere temporary variations, such as size, albinism, etc., the more permanent varieties are generally found, as far as I can judge, *inhabiting distinct stations, high land or low land, dry or moist districts, or distinct regions.*"†

In the portions of these passages which I have distinguished by italics, Darwin seems clearly to maintain that for the formation of coexistent permanent varieties some degree of local separation is necessary. I therefore conclude that when he says, he cannot regard migration and isolation as necessary for

* The same passages occur in the sixth edition, pp. 80, 81.

† In the sixth edition this passage will be found, slightly modified, in Chapter VII, p. 169.

the formation of new species he intends to express, in opposition to Moritz Wagner, the opinion that a species may be transformed into a new species without leaving its original locality, but that he does not intend to say, that two or more divergent species can arise in the same locality from the same stock. If I interpret him rightly he considers the partial separation described in the first of the paragraphs just quoted as sufficient to allow of the formation of divergent species, when the external conditions of the separate districts are sufficiently different and sufficiently permanent to secure long continued divergent natural selection. That the second paragraph is to be interpreted in accord with this meaning I judge from the fact that natural selection is mentioned here as the cause of the divergence which crossing tends to overpower, and in the third paragraph, uniformity in the environment is represented as ensuring uniform natural selection. The varieties that are restrained from crossing with each other by diverse times and habits of breeding, he must regard, sometimes as slightly divergent forms tending to disappear under the pressure of uniform natural selection, and therefore never becoming separate species though one of them may prevail and be established as a new species; and sometimes as forms that are becoming more and more divergent, because they have found their way into districts or stations where they are somewhat separated from each other, and where the conditions are somewhat different, and the natural selection, therefore, somewhat diverse.

If this is not his meaning, if he intends to teach that forms arising in one place and not locally separated from each other can continue to diverge till they become separate species, how can he say on the next page that forms isolated in a small area, being exposed to uniform conditions, would be modified by natural selection in a uniform manner. He evidently does not intend to be understood as teaching that in these cases mentioned in the second paragraph there is a cause of divergent evolution which produces separate varieties and species in spite of the unifying influence of natural selection resulting from uniform conditions.

Darwin's Theory of Natural Selection through the Advantage of Divergence of Character.

There is however, one passage in the "Origin of Species" which may be interpreted as assigning a cause for divergence of character in representatives of the same species that are surrounded by the same environment. These are the words; "Only those variations which are in some way profitable will be preserved, or naturally selected. And here the importance

of the principle of benefit being derived from divergence of character comes in; for this will generally lead to the most different or divergent variations being preserved and accumulated by natural selection." (*Origin of Species*, Chap. IV, first page of the section on the "Probable Results of the Action of Natural Selection, through Divergence of Character and Extinction in the Descendants of a Common Ancestor." In the sixth edition, this passage occurs on pp. 90-1). The connection in which this passage stands seems to indicate that "the benefit derived from the divergence of character" is considered the cause of "the most different or divergent variations being preserved and accumulated by natural selection," even in the case of the representatives of the same species that are competing with each other on the same area, and are in no way prevented from intercrossing. It is therefore necessary to show the difficulties that beset such a theory, especially if we adhere to the more general theory, that diversity in the kinds of natural selection affecting a species must be due to differences in the environments by which it is surrounded.

In the first place, natural selection, which is the superior propagation of those best adapted to the environment, prevents the interbreeding of the adapted forms that propagate with the unadapted that fail of propagating; but it can never prevent the interbreeding of those forms which through different kinds of adaptation to the environment survive and propagate, and, therefore, it can have no influence in producing accumulated divergence, unless it is supplemented by some segregative principle that prevents the different kinds of adaptations from being interfused. In the second place, as long as we follow Darwin's explanation of the causes of natural selection, we must hold that the representatives of one species while surrounded by the same environment, whether prevented from intercrossing or not, will, through the uniform action of natural selection, be modified in the same way, if at all, and, while surrounded by distinct and dissimilar environments, will be modified in divergent ways; but, in this latter case, as they will be prevented from competing with each other by occupying different areas, they can derive no advantage from divergence of character through its preventing competition, therefore the divergence that follows must be attributed to some other cause. In other words, the advantage attributed by Darwin to divergence of character is freedom from competition, through diversity of adaptation, and, as some degree of prevention of crossing is necessary for permanent difference in adaptations, the advantage cannot be secured unless there is some cause preventing the crossing of the divergent forms. Now, the prevention of crossing, if it ever arises, will be secured

either while the individuals that are prevented from interbreeding are occupying the same limited area and exposed to the same environment, or while occupying distinct areas and exposed to either the same or different environments. In the first case, we are told by Darwin, that exposure to uniform conditions "will tend to modify all the varying individuals of the same species in the same manner." In the second case, as the sections of the species that are prevented from crossing occupy separate areas, the advantage of freedom from competition is already secured without divergent adaptation, and there can be no further advantage of that kind.

Again, it is not difficult to show that divergence is in itself no benefit, for multitudes of more divergent forms fail, leaving the field to less divergent ones. This is generally true of monstrosities, and frequently true of other kinds of variations. Neither can it be claimed that freedom from competition is an advantage unless it results in freer access to unappropriated resources, and this advantage is most frequently gained by migrating into a locality presenting the same environment but not previously occupied by the species. In this last case, the access to unappropriated resources does not depend on new adaptations; and, as any new adaptations that might bring advantage to the representatives of the species in one district would be of equal advantage in the other district, no divergence of character could be advantageous. It is this impossibility of advantage in divergence of character in portions of a species exposed to the same environment which leads many naturalists to maintain that isolation does not tend to produce divergence unless accompanied by exposure to different environments. But their reasoning is inconclusive inasmuch as they have never shown that divergence depends on its being advantageous. In my study of Sandwich Island molluscs I have found very strong reasons for believing that divergence may arise in the representatives of one species during exposure to the same environment, producing not only non-adaptive, but also adaptive differences. But whether adaptive or non-adaptive, whether due to natural selection or to some other principle, differences that arise under the same environment cannot be advantageous differences, and the divergence through which the differences are reached is not advantageous divergence. It seems to me evident that, neither is divergence always advantageous, nor is the advantage of access to unappropriated resources necessarily dependent on divergence; that, neither does the accumulation of divergence depend on its being advantageous, nor is advantageous divergence always accumulated.

Darwin's Theory that Exposure to Different Environments is Essential to diversity of Natural Selection.

Diversity of natural selection in different portions of the same species depends upon diversity in the relations of the different portions to the environment. Now, observation shows that cumulative diversity in the relations of the species to the environment may be introduced, (1) by dissimilar changes in the environment presented by the different areas occupied by the different portions; (2) by different portions of the species entering different environments; or (3) by dissimilar changes in the habits of the different portions of the species in using the same environment. Certainly in this third class of cases, if not in the other classes, without prevention of free crossing between the different portions, there can be no cumulative diversity in relations to the environment, and therefore no cumulative diversity in the natural selection; and without the same condition, there can be no accumulation of divergent effects of natural selection, in any case. Darwin, however, forgetting the possibility of divergent changes in the habits of isolated portions of a species exposed to the same environment, maintains that exposure to different environments is essential to diversity of natural selection and to divergence. Without change in the climate, soil, or organic forms lying outside of the species there is, according to him, nothing to produce modification.

"If a number of species after having long competed with each other in their old home were to migrate in a body into a new and afterwards isolated country, they would be little liable to modification; for neither migration nor isolation in themselves effect any thing. These principles come into play only by bringing organisms into new relations with each other, and in a lesser degree with the surrounding physical conditions."—[Origin of Species. On the 4th and 5th pages of the first chapter on Geographical Distribution.]* "Each separate island of the Galapagos Archipelago is tenanted, and the fact is a marvelous one, by many distinct species; but these species are related to each other in a very much closer manner than to the inhabitants of the American continent, or of any other quarter of the world. This is what might have been expected, for islands situated so near each other would almost necessarily receive immigrants from the same original source, and from each other. But how is it that many of the immigrants have been differently modified, though only in a small degree, in islands situated within sight of each other, having the same geological nature, the same height, climate, etc.?" This long

* See ed. 6, p. 319.

appeared to me a great difficulty; but it arises in chief part from the deeply seated error of considering the physical conditions of a country as the most important; whereas it cannot be disputed that the nature of the other species with which each has to compete, is at least as important, and generally a far more important element of success. Now if we look to the species which inhabit the Galapagos Archipelago, and are likewise found in other parts of the world, we find that they differ considerably in the several islands.”—[*Origin of Species*, near the middle of the second chapter on Geographical Distribution.]*

The implication in both these passages is that if the representatives of the same species are surrounded by the same organic forms as well as by the same physical conditions in isolated countries, they will not undergo divergent modification. This is in complete accord with the third paragraph quoted near the beginning of this paper from the 4th chapter of the “*Origin of Species*.”

Divergent Forms of Sexual Selection.

In the passages last quoted there is no mention of any exception to the principle that difference in external conditions is necessary to divergent evolution. No suggestion is given that through the action of sexual selection divergent species may be produced that are not at all dependent on differences in the environments, still there can be no doubt that this was Darwin's view. Though he does not directly discuss this problem in any passage I have been able to discover, he clearly expresses the opinion that the differences between the different races of man, and between man and the lower animals, are in no small degree due to sexual selection, and he never speaks of difference in sexual selection as depending on difference in the environment, though, at the close of the twentieth chapter of “*The Descent of Man*,” he speaks of sexual selection in man as having probably “exaggerated” the “characteristic qualities” “which are of no service to” the tribes and races that possess them. The differences, however, in the races of man are attributed to sexual selection, not because of any lack of difference in their environments, but because the characters in which they differ do not seem to him to be related to the environment. The color of the skin, hair, and eyes, and the different forms of the head and face do not seem to be adapted to different conditions in the environment, while they are undoubtedly occasions of attraction or aversion for those seeking partners. He has not, however,

* See ed. 6, p. 355.

shown whether the change of taste precedes the change of form and color, or the reverse. Differences between the sexes of the same species in secondary sexual characters, are for weighty reasons attributed to sexual selection; but he does not show how this divergence between the sexes leads to the production of new species. This production of difference of character between the sexes, being in no way dependent on the prevention of crossing between the divergent sexes, must be a wholly different process from the production of races and species, which is absolutely dependent on prevention of crossing between the divergent races and species. There is, nevertheless, every reason to believe that when the representatives of a species capable of sexual selection are for many generations separated into groups that never cross, diversity of tastes is one of the forms of diversity that inevitably arises; but that the psychological divergence is the cause of the other correlated divergences is not so certain. The theory of divergence in races because of divergence in the forms of sexual selection seems to rest on the assumption that a psychological divergence may be accumulated and rendered permanent in a new and definite form without being subjected to selection; but if this is true of a psychological divergence, why may it not be true of any form of divergence? The difference in the ideals of beauty in different races is as important as difference in the skin and hair; and in accounting for the origin of races, it is quite as important to account for the former as for the latter; any theory that simply attributes the difference in the color of the skin to difference in the ideal of beauty, will be met by the suspicion that the difference in the ideal was preceded by the difference in the color. My own strong conviction is that the true explanation is equally applicable to either set of phenomena.

Darwin's reference to the Causes which Check the Crossing of Varieties.

In the second paragraph quoted from Darwin at the beginning of this chapter we find mention of three causes that may for a long time prevent the members of the same species from freely intercrossing while occupying the same area; but subsequent statements, in the same and the three succeeding sections, show that he regarded geographical and local separation as the forms of separate breeding that are most favorable to the production of new species. Moreover, in the two sections relating to "Divergence of Character," he seems to maintain that the prevention of intercrossing is not a necessary condition for divergence of character in members of the same

species that are competing with each other.* In chapter XVI, of his "Variation under Domestication" several causes that interfere with the free crossing of varieties are enumerated; but they are nowhere recognized as essential factors in the evolution of divergent varieties and species, without which diversity of natural selection would be of no avail, and with which divergence will take place though there is no change in the environment. They are looked upon as characteristics in which many varieties more or less resemble species; but they are regarded as the results rather than the causes of divergent evolution.

Conclusion.

We, therefore, find that though Darwin has not recognized segregation, which is the independent propagation of different variations, as a necessary condition for the production of divergent races and species, he has pointed out one process by which segregation is produced in nature. This one process is geographical or local separation under different environments. It may be the result of migration, or of geological and other changes in the environment; but, in either case, there is the preservation of different variations through diversity of natural selection due to the difference in the environments, and the independent propagation of the same variations due to their geographical or local separation. We have in this process an important cause of segregation resulting in divergent evolution; but no one can maintain that this is the only cause producing segregation and divergence, unless he ignores the fact that, in some cases, the isolated portions of a species, while exposed to the same environment, acquire divergent habits in the use of the environment, producing diversity of natural selection; and that, in other cases, without exposure to different environments, the very process producing the isolation, brings together those of one kind preventing them from crossing with those of other kinds, as when individuals of a special color prefer to pair together. In the former cases, indiscriminate separation is transformed into Segregation; and, in the latter cases, the isolation is segregative from the first; while, in both classes of cases, the divergence is without exposure to different environments.

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*In "Nature," vol. xxxiv, page 407, Mr. Francis Darwin states that in his copy of Belt's "Naturalist in Nicaragua" the words "No, No," are penciled in his father's handwriting on the margin, opposite the sentence: "All the individuals might vary in some one direction, but they could not split up into distinct species whilst they occupied the same area and interbred without difficulty." This seems to give a decisive answer concerning Darwin's opinion on this subject.