NEITHER Mr. Galton nor Mr. Meldola have had time or opportunity to consult my original paper before writing their comments on the NATURE abstract. I will, therefore, consider those of their remarks which have been anticipated in the paper.

Mr. Galton writes:—"It has long seemed to me that the primary characteristic of a variety resides in the fact that the individuals who compose it do not, as a rule, *care to mate* with those who are outside their pale, but form through their own sexual inclinations a caste by themselves." Now, I have fully recognised this principle as one among several others which is accessory to, although independent of, physiological selection: see L.S. paper, p. 377, where also reference is given to the "Origin of Species," showing that this factor was likewise recognised by Mr. Darwin as one of importance in the prevention of intercrossing. But, inasmuch as this factor—which may be called psychological selection—can only apply to the case of the Vertebrata,[1] I am disposed to think that it is of much less general importance than the other factors which I have mentioned as accessory to physiological selection, and which, taken altogether, furnish a complete theoretical explanation of the fact that sterility between natural species is not invariably absolute, but occurs in all degrees. For, "in all these cases where the principles of physiological selection have been in any degree accidentally assisted by other conditions, a correspondingly less degree of variation in the reproductive system would have been needed to differentiate the species" (p. 377).

Thus far, therefore, Mr. Galton is really in full agreement with me. But he goes on to say:—"If a variety should arise in the way supposed by Mr. Romanes, merely because its members were more or less infertile with others sprung from the same stock, we should find numerous cases in which members of the variety consorted with outsiders." But how can we possibly know that such is not the case? If my theory is true, it must follow, as Mr. Galton says, that such unions would be more or less sterile, and, as this sterility is itself the only variation which my theory supposes to have arisen *in the first instance*, *ex hypothesi* we can have no means of observing whether or not the individuals which present this variation "consort with outsiders," or with those individuals which do not present it. Lastly, in as far as it is true that "we hardly ever observe pairings between animals of different varieties when living at large in the same or contiguous districts," the fact in no way makes against my theory of physiological selection: it only serves to supplement this theory, in the case of higher animals, by what I regard with Mr. Galton as the proved facts of psychological selection.

The letter by Mr. Meldola is a masterpiece of Darwinian thinking, and on this account I am glad to find myself much more in agreement with him than he appears to suppose. For when he reads my full paper he will see that I have taken precisely the same view upon natural selection as a possible cause —or, rather, accessory promoter—of specific sterility as that to the statement of which the larger part of his letter is devoted. I may remark, however, that of all parts of my paper I regard this as the most speculative and least secure. And this, first, because Mr. Darwin himself, after profound meditation upon the subject, came to the conclusion that natural selection could not operate so as to induce sterility; and, next, because the supposition that it does so operate involves one of the most difficult and complex questions in the whole philosophy of evolution—namely, whether it is possible for natural selection to modify an entire *type* without reference to benefit of its constituent *individuals*. Now, although for reasons which need not here be detailed, I have been led, like Mr. Meldola, to take a different view from that of Mr. Darwin, and to conclude that natural selection may benefit the type without reference to the individual, still I regard this conclusion as so highly speculative that I am glad to think the much more certain theory of physiological selection is not vitally affected either by its acceptance or its rejection. If it is true that natural selection may be able to modify an organic type (as my critic and myself agree in arguing, the type in this case being a variety) by conferring on it the benefit of sterility with its parent form, notwithstanding that this cannot be effected through benefit conferred on any of the constituent individuals, then all we have to say in the present connection is that natural selection is probably one of the many other causes which lead to physiological selection.

[1] This, at least, is what I state in the paper. Mr. Galton, however, suggests that the principle may be extended even to plants, through "the selective appetites of the insects which carry the pollen." This suggestion is unquestionably original, and bears the stamp of its author's ingenious mind. Moreover, considerable probability is, I think, lent to the suggestion by the observations of Mr. Bennett and others on individual insects selecting similarly coloured flowers on which to feed (see *Journ. L.S.*, 1883).

On the other hand, if natural selection cannot thus operate, all we have to say is that there still remain many other causes adequate to explain the occurrence of physiological selection—to wit, those causes which are concerned in the occurrence of variation in general.

The essay by Prof. Weismann on the influence of isolation, to which Mr. Meldola refers, is so replete with facts and arguments unconsciously bearing on my theory, that in writing my preliminary paper it appeared advisable to reserve so rich a mine for subsequent working out in detail. In my paper, therefore, I have merely alluded to Prof. Weismann as one among the comparatively few evolutionists who have hitherto sufficiently considered the influence of independent variation (or the prevention of intercrossing) in the evolution of species.

It only remains to consider Mr. Meldola's extremely able criticism of my view that natural selection ought not in strictness to be regarded as a theory of the origin of species, but rather as a theory of the development of adaptive modifications. My argument is that natural selection can only be a theory of the origin of species in so far as species differ from one another in points of utilitarian significance; and that even then it is only a theory of the origin of species, as it were, incidentally: the *raison d'être* of natural selection is in all cases that of evolving adaptations (whether these be characteristic of species only, or likewise of higher taxonomic divisions); and if in some cases the result of performing this function is that of raising a variety into a species, such a result is merely collateral, or, in a sense, accidental. No doubt if species always and only differed from one another in points of utilitarian character, the collateral nature of the result might be disregarded, and the theory would become a theory of the origin of species in virtue of its being a theory of the development of adaptations. But, as a matter of fact, species are very far from being always and only distinguished from one another in points of utilitarian character, and in so far as they are not thus distinguished natural selection is obviously in no sense a theory of the origin of species. Again, and more particularly, the one feature which more than any other serves to distinguish species from species is that of mutual sterility, and it would be a bold flight of speculation to affirm that this has been in all cases the result of natural selection, when even Mr. Darwin was reluctantly compelled to conclude that such could not be the result of natural selection in any case. On the other hand, my theory of physiological selection explains this very general feature of specific distinction quite independently of natural selection; and then goes on to show that, when once this primary distinction has arisen, many others of a secondary kind will ensue, both with and without the assistance of natural selection.

Now, the objection which Mr. Meldola adduces against this argument is that I have not proved physiological selection to be independent of natural selection. In other words, he does not dispute the probable truth of my theory; but he says that, granting its truth, it is still only "one particular phase of natural selection." But surely the burden of proof here lies on the side of my critic. If he can show any sufficient reason for going much further than I have ventured to go in out-Darwining Darwin—or for holding that natural selection may not merely help in inducing sterility in some cases, but has been the sole cause of it in all cases—then I should welcome his proof as showing that the principles of physiological selection ultimately and in all cases rest on those of natural selection. But, clearly, it is for him to prove his positive: not for me to prove what I regard as an almost preposterous negative.

So much for the main criticism. But he adds this rider, namely, that, as the struggle for existence is always most severe between the most closely related forms, unless the new or sexually protected form arising under physiological selection possesses some distinct advantage over the old or parent form, it will be exterminated by the latter quite as effectually as it would be by intercrossing in the absence of physiological selection. To this I may answer in the words of my full paper:—"So long as there is no actual *detriment* arising to the variety on account of its being sexually separated from the parent, any ideas derived from the theory of natural selection are plainly without bearing upon the subject" (p. 406). In other words, so long as in all other respects of organisation the sexually separated variation is not less "fit" than its parent stock, so long there is no reason to anticipate any disadvantage in the struggle for existence. And forasmuch as the sexual separation arises only by way of a variation locally affecting the reproductive system, when the variation is first sexually separated, it will in all other respects resemble its parent stock, and so be able to compete with it on equal terms—mere numerical inferiority being without significance where intercrossing is prevented. It was in order to convey this meaning that I proposed as an alternative name of my theory, "Segregation of the Fit"; seeing that before any physiological segregation can take place there must be organisms to be segregated, and that unless these organisms had already proved themselves fitted to survive in the struggle for existence, in existence they could not be. But I do not call physiological selection "Segregation of the *Fittest*," because, unlike natural selection, it is in no way concerned with the principle of conflict. So long as the organisms which have been separated by physiological selection are sufficiently fit to have previously passed muster at the hands of natural selection, there is no reason why the daughter type should be fitter than the parent.

But, so far as I can see, the only material point of difference between Mr. Meldola and myself consists in his regarding physiological selection as "subordinate" to natural selection, while I consider the two as quite independent principles, although, as explained in my paper, I believe that they frequently and in several ways play into each other's hands.

GEORGE J. ROMANES

Geanies, Ross-shire, N.B., August 30

Physiological Selection and the Origin of Species

SEEING that criticisms on the theory of physiological selection are flowing through channels other than the pages of NATURE, and this in a volume larger than could at first have been anticipated, it seems desirable that I should now permit them to exhaust themselves before undertaking a further and a general reply. On the present occasion, therefore, I will only ask you to be good enough to insert the following remarks.

In order to put myself right with my critics, I should like them to remember that the paper published by the Linnean Society is designedly restricted to a preliminary statement of principles, which, it was hoped, might fulfil its avowed object of inducing other naturalists to co-operate with me in verifying the theory by observation and experiment, in the ways suggested. Such being the design, all details as to facts and references were intentionally omitted, and the same has to be said for all objections to the theory which had occurred to my own mind. All these things will require to be gone into with the utmost care, should the course of verifying inquiry eventually prove that the voice of Nature pronounces for the theory. Therefore, while I shall be thankful for all criticisms, I should like my critics to remember that they have not as yet my whole case before them. In particular, I may intimate that I should not have published even the outlines of my theory had I not been prepared for the very obvious exceptions which are taken to it by Mr. Wallace in the current issue of the *Fortnightly Review*.

I am much indebted to Mr. Francis Darwin for his reference to Mr. Belt's anticipation of my theory, for the fact that in its general form this theory has independently occurred to so distinguished a naturalist, appeals to me as an additional pledge of its probability. On the other hand, I am greatly disheartened by his further statement that he has reason to suppose his father was "familiar with the principle of physiological selection," and yet "did not regard it with any great favour." Hitherto I have been under the impression that it was a theory to which the judgment of his father would probably have inclined, and therefore I shall await with no ordinary interest the statement of his reasons for thinking otherwise, whether this be communicated through your columns or privately to myself. It only remains to add that, if Mr. Darwin will be kind enough to turn to p. 380 of my paper, he will find that I have quoted *in extenso*, and with its context on both sides, the passage from the "Origin of Species" which he extracts. But it does not appear to me that this passage furnishes any evidence that the theory of physiological selection was ever present to the mind of the writer—less evidence, for instance, than there is from a passage in one of his earliest writings that the theory of natural selection was present to the mind of Mr. Herbert Spencer.

GEORGE J. ROMANES

Geanies, Ross-shire, September 4