PHYSIOLOGICAL SELECTION: AN ADDITIONAL SUGGESTION ON THE ORIGIN OF SPECIES[1]

I.

THERE are three cardinal difficulties in the way of natural selection, considered as a theory of the origin of species.

(1) The difference between species and varieties in respect of mutual fertility. Many of our domesticated varieties differ from one another to an extent greater than that which distinguishes many natural species: yet they continue perfectly fertile *inter se*, while the natural species are nearly always more or less sterile. The difficulty is not met by pointing to the fact that sterility between natural species is neither absolutely constant nor constantly absolute; for the question still remains, Why are the modifications of organic types supposed to have been produced by natural selection, so generally attended with some more or less pronounced degree of mutual sterility, when even greater modifications of such types produced by artificial selection so generally continue mutually fertile? That this question does not admit of any answer by the theory of natural selection Mr. Darwin himself acknowledges, and therefore suggests a wholly independent hypothesis by which to explain the fact. This hypothesis is, that varieties occurring under nature "will have been exposed during long periods of time to more uniform conditions than have domesticated varieties, and this may well make a wide difference in the result." Now, whatever we may think of this hypothesis, it is certainly quite distinct from the theory of natural selection; and, therefore, any one who adopts the supplementary hypothesis is, so far, confessing the inadequacy of that theory, considered as a theory of the origin of species. For my own part, I deem the hypothesis wholly insufficient to meet the facts. When we remember the incalculable number of species, living and extinct, we immediately feel the necessity for some much more general explanation of their existence than is furnished by supposing that their mutual sterility, which constitutes their most general or constant distinction as species, was in every case due to some incidental effect produced on the generative system by uniform conditions of life. To say nothing of the antecedent improbability that in all these millions and millions of cases the reproductive system should happen to have been affected in this peculiar way by the merely negative condition of uniformity, there remains what seems to me the overwhelming consideration that, at the time when a variety is first forming, the condition of prolonged exposure must necessarily be absent as regards that variety: yet this is just the time when we must suppose that the infertility with its parent form arose. Because, if not, the incipient variety would have been reabsorbed into its parent form by intercrossing.

(2) For the swamping effects of free intercrossing upon an individual variation constitutes the next, and perhaps the most formidable, difficulty with which the theory of natural selection is beset. The only answer which Mr. Darwin has to make in this case is that a number of individuals inhabiting the same area may vary in the same way at the same time. Of course, if this assumption were granted, there would be an end of the present difficulty; for if a sufficient number of individuals were thus similarly and simultaneously modified, there need no longer be any danger of the variety being swamped by intercrossing. But the force of the difficulty consists in the very fact of this assumption being required to meet it. The theory of natural selection trusts to the chapter of accidents in the matter of variation; and in this chapter we read of no reasons why the same beneficial variation should arise in a number of individuals simultaneously. Moreover, if it does so, the fact of its doing so cannot be attributed to natural selection, which thus again fails as a theory of the origin of species. Lastly, as will immediately be shown, a very large proportion, if not the majority, of features which serve to distinguish species from species, are features presenting no utilitarian significance; and, therefore, even if it be conceded that they each arose in a number of individuals simultaneously, their reabsorption by intercrossing could not have been in any degree hindered by natural selection.

(3) The difficulty just alluded to of the inutility to species of so large a proportion of specific distinctions, is one which Mr. Darwin frankly acknowledges in the later editions of his works. In other words, he allows that a large proportion of these distinctions resemble the more general distinction of sterility in not admitting of any explanation by the theory of natural selection. They consist of small and trivial differences of form and colour, or of meaningless details of structure, which, being of no service to the plants or animals presenting them, cannot have arisen through the agency of natural selection. If it be suggested that all such distinctions are of disguised utility, the answer is that to offer this suggestion is to reason in a circle. For the only evidence we have of natural selection as an operating cause in any case is derived from the utility of the observed results: therefore, in cases where utility is apparently absent, we may not assume that it must be present only because, if it were not present, the results must be due to some cause other than natural selection. Observe, the case would be different if the great majority of specific distinctions—like the great majority of higher distinctions—were of obvious utilitarian significance; for in this case we might reasonably set down the exceptions as proof of the rule, or hold that they appear to be exceptions only on account of our ignorance. But it is certainly too large a demand on our faith in natural selection to appeal to the argument from ignorance when the facts require that the appeal should be made over so very large a proportion of instances. But it is needless further to insist upon this

[1] Abstract of a Paper read before the Linnean Society on May 6, by George J. Romanes, M.A., LL.D., F.R.S. &c.

point, since, as I have already observed, its force has been fully recognised by Mr. Darwin and his followers. Here again, therefore, the theory of natural selection fails as a theory of the origin of species.[1]

In view of these three grave disabilities under which the theory of natural selection lies, I feel entitled to affirm that the theory has been misnamed. Natural selection is not, properly speaking, a theory of the origin of *species:* it is a theory of the origin—or rather of the cumulative development—of *adaptations*, whether these be morphological, physiological, or psychological; and whether they occur in species only, or likewise in genera, families, orders, or classes. These two things are very far from being the same; for, on the one hand, in an enormously preponderating number of instances, adaptive structures are common to numerous species, while, on the other hand, the features which serve to distinguish species from species are, as we have just seen, by no means invariably —or even generally—of any adaptive character. If once it is thus clearly perceived that the theory of natural selection is not a theory of the origin of species, but a theory of the development of adaptive structures—whether these happen to be distinctive of species or of higher taxonomical divisions—if once this is clearly perceived, the theory is released from all the difficulties which we have been considering. For these difficulties have beset the theory only because it has been made to pose as a theory of the origin of species, whereas in point of fact it is nothing of the kind. In so far as natural selection has had anything to do with the genesis of species, its operation has been, so to speak, incidental: it has only helped in the work of originating species in so far as some among the adaptive variations which it has preserved happen to have constituted differences of merely specific value. Many other such differences there are with which natural selection has had nothing to do—particularly the most universal of all such differences, or that of mutual sterility —while, on the other hand, by far the larger number of adaptations which have been the work of natural selection are now the common property of genera, families, orders, or classes. Let it, therefore, be clearly understood that it is the office of natural selection to evolve adaptations: not necessarily, or even generally, to originate species.

Let it also be clearly understood that in thus seeking to place the theory of natural selection on its true logical footing, I am in no wise detracting from the importance of that theory. On the contrary, I am but seeking to release the theory from the difficulties with which it has been hitherto illegitimately surrounded.

Enough has now been said to justify the view that there must be some cause or causes other than natural selection operating in the evolution of species. And this is no more than Mr. Darwin himself has expressly and repeatedly stated to have been his own view of the matter; nor am I aware that any of his followers have thought otherwise. Hitherto the only additional causes of any importance that have been assigned are use and disuse, sexual selection, correlated variability, and yet another principle which I believe to have been of much more importance than any of these. Yet it has attracted so little attention as scarcely ever to be noticed by writers on evolution, and never even to have received a name. For the sake of convenience, therefore, I will call this principle the Prevention of Intercrossing with Parent Forms, or the Evolution of Species by Independent Variation.

First let us consider how enormous must be the number of variations presented by every generation of every species. According to the Darwinian theory 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, we might expect that new varieties (for the most part of a trivial and unuseful kind) should arise within that section, and that in time these varieties should pass into new species. And this is exactly what we do 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 of such an island permits them to develop independent 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. When a species begins to disperse in different directions from its original home, those members of it which constitute the vanguard of each advancing army are much more likely to perpetuate any individual variations that may arise among them than are the members which still occupy the original home. For not only is the population much less dense on the outskirts of the area occupied by the advanced guard; but beyond these outskirts there lies a wholly unoccupied territory, upon which the new variety may gain a footing during the progress of its further migration. Thus, instead of being met on all sides by the swamping effects of intercrossing with its parent form, the new variety is now free to perpetuate itself with comparatively little risk of any such immediate extinction. And, in the result, wherever we meet with a chain of nearly allied specific forms so distributed as to be suggestive of migration with continuous modification, the points of specific difference are trivial or non-utilitarian in character. Clearly this general fact is in itself enough to prove that, given an absence of overwhelming intercrossing, independent variability may be trusted to evolve new species. The evidence which I have collected, and am collecting, of the general fact in question, must be left to constitute the subject of a future paper.[1]

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 separated from one another by geographical barriers, one might reasonably be disposed to 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 by the influence of natural selection. The object of the present paper is to suggest an additional factor in the formation of specific types by independent variability, and one which appears to me fully competent to explain both the general facts just mentioned.

[1] Of the three cardinal objections to the theory of natural selection thus briefly stated, Mr. Darwin himself appears to have attributed most importance to the first, seeing that its consideration occupies so large a portion of his writings. The objection from intercrossing, on the other hand (which was first rendered with much force and clearness by the late Prof. Fleeming Jenkin of Edinburgh, in an anonymous article, *North British Review*, 1867), is the only difficulty in the way of his theory which Mr. Darwin can fairly be said not to have sufficiently treated. The objection from inutility was first prominently raised by Bronn. It was afterwards developed by Nägeli, Broca, Mivart, and many other writers.

[1] So far as I am aware, the first writer who insisted on the importance of the prevention of intercrossing in the evolution of species, both by isolation and migration, was Moritz Wagner. Since then Wallace, Weismann, and others have recognised this factor. The most recent contribution to the subject is an admirable collection of facts published by Mr. Charles Dixon in a work entitled, "Evolution without Natural Selection," which was recently reviewed in these columns. But I cannot find that any of these writers allude to the principle which it is the object of the present paper to enunciate, and which is explained in the succeeding paragraphs.

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 of diminished fertility. Having, regard, therefore, to all the delicate, complex, and for the most part hidden conditions which determine this double kind of variation within the limits of the reproductive system, there can be no difficulty in granting that variations in the way of greater or less sterility must frequently occur both in plants and animals in a state of nature. Probably, indeed, if we had the 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. But now, if the variation should be such that, while showing some degree of sterility with the parent form, it continues to be perfectly fertile within the limits of the varietal form, in this case the variation would neither be swamped by intercrossing, nor would it die out on account of sterility. On the contrary, this particular variation would be perpetuated with more certainty than any other variation, whether useful or unuseful. An illustration will serve to render this more clear.

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, as we say, spontaneous, or due to any change of food, climate, habitat, &c., does not signify. The only point we need here attend to is that some individuals, living on the same geographical area as the rest of their species, have varied in their reproductive systems so that they are perfectly fertile *inter se*, while absolutely sterile with all other members 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 is that the barrier, instead of being geographical, is physiological.

From this illustration I hope it will be obvious that wherever any variation in the highly variable reproductive system occurs, tending to sterility with the parent form without impairing fertility with the varietal form—no matter whether this be due, as here supposed, to a slight change in the season of reproductive activity, or to any other cause—there the physiological barrier in question must interpose, with the result of dividing the species into two parts. And it will be further evident that when such a division is effected, the same conditions are furnished to the origination of new species as are furnished to any part of a species when separated from the rest by geographical barriers or by migration. For now the two sections of the species, even though they be living on the same area, are free to develop distinct histories without mutual intercrossing, or, as I have phrased it, by independent variation.

To state this suggestion in another form. It enables us to regard many, if not most, natural species as the records of variation in the reproductive systems of ancestors. When accidental 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 inevitably tend to be preserved as new natural varieties, or incipient species. At first the difference would only be in respect of the reproductive system; 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, as I will show later on. For the sake of convenience, therefore, and in order to preserve analogies with already existing terms, I will call this principle Physiological Selection, or Segregation of the Fit.

Before proceeding to state the evidence of the particular kind of variation on which this principle depends, let it be noted that we are not concerned either with its causes or its degrees. Not with its 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 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 in the long run be 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.

(*To be continued.*)

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II.

NEXT, let it be observed that we cannot expect to meet with much direct evidence of physiological selection from our domesticated varieties. For, first, breeders and horticulturists keep their strains separate artificially, and preserve many kinds of variation other than those of the reproductive system with which alone we are concerned; and, secondly, it is never the aim of these men to preserve this particular kind of variation. Therefore, all that we can here learn from our domesticated productions is the paramount importance of preventing intercrossing with parent forms, if a new varietal form is ever to gain a footing. No one of these domesticated varieties could have been what it now is unless such intercrossing had been systematically prevented by man; and this gives us good reason to infer that no natural species could have been what it now is unless every variety in which every species originated had been prevented from intercrossing with its parent form by nature. For the cases are extremely rare in which one species differs from another (living or extinct) in respect of any feature so highly utilitarian in character as to justify belief that the newer species owed its differentiation to natural selection having been able to overcome the swamping effects of free intercrossing.

[1] Abstract of a Paper read before the Linnean Society on May 6, by George J. Romanes, M.A., LL.D., F.R.S. &c. Continued from p. 316.

Again, as to plants and animals in a state of nature, the particular variation with which we are concerned would scarcely be noticed until it had given rise to a new species. In this respect, therefore, the theory of physiological selection is in the same predicament as that of natural selection: in neither case are we able directly to observe the formation of one species out of another by the agency supposed; and, therefore, in both cases our belief in the agency supposed must to a large extent depend on the probability established by general considerations. Nevertheless, although our sources of direct evidence are thus seen to be necessarily limited, I shall now hope to show that they are sufficient to prove the only fact which they are required to prove—namely, that the particular kind of variation, on the occurrence of which my theory depends, does occur both in nature and under domestication.

One very obvious example of the particular variation which is required by the theory of physiological selection has already been given in the season of flowering or of pairing being either advanced or retarded. This I take to be a most important case for us, inasmuch as it is one that must frequently arise in nature. Depending as it chiefly does on external causes, numberless species both of plants and animals must, I believe, have been segregated by its influence. For in every case where a change of food, temperature, humidity, altitude, or of any of the other many and complex conditions which go to constitute environment—whether the change be due to migration of the species or to alterations going on in an area occupied by a stationary species—in every case where such a change either retards or promotes the season of propagation, there we have the kind of variation which is required for physiological selection. And it is needless to give detailed instances of such variation where this is due to so well known and so frequently observed a cause.

But it is on what may be called the spontaneous variability of the reproductive system itself that I mainly rely for evidence of physiological selection. The causes of variability are here much more numerous, subtle, and complex than are such extrinsic causes as those just mentioned; and they are always at work in the reproductive systems of all organisms. The consequence is, as Mr. Darwin has shown by abundant evidence, that variations in the direction of sterility depend more on what he calls the nature of the organism than on the influence of external conditions. Of this fact we have direct evidence, firstly in individuals, secondly in varieties, and thirdly in species.

(1) *Individuals.*—Mr. Darwin observes, "it is by no means rare to find certain males and females which will not breed together, though both are known to be perfectly fertile with other males and females. We have no reason to suppose that this is caused by these animals having been subjected to any change in their habits of life; therefore such cases are hardly related to our present subject. The cause apparently lies in an innate sexual incompatibility of the pair when matched." He then proceeds to give examples from horses, cattle, pigs, dogs, and pigeons, concluding with the remark that "these facts are worth recording, as they show, like so many previous facts, on what slight constitutional differences the fertility of an animal often depends." Elsewhere he gives references to similar facts in the case of plants; and instances of this individual incompatibility, both in plants and animals, might easily be multiplied.

Now, if even as between two individuals there may thus arise absolute sterility without there being in either of them the least impairment of fertility towards other individuals, much more may such incompatibility extend towards a number of individuals. For certainly the most remarkable feature about this individual incompatibility is the fact of its being only individual: it would not be nearly so remarkable, or antecedently improbable, if the incompatibility were to run through a whole race or strain. In the fact of individual incompatibility, therefore, we have the kind of variation which my theory requires, and this as arising spontaneously in the highest degree of efficiency.

(2) *Races.*—But of even more importance for us is the direct evidence of such a state of matters in the case of varieties, breeds, or strains. In the ninth chapter of the "Origin of Species," and in the nineteenth chapter of the "Variation of Plants and Animals under Domestication," Mr. Darwin adduces miscellaneous instances of varieties of the same species which exhibit a higher degree of fertility within themselves than they do with one another. In this respect, therefore, they resemble natural species; but as they are only domesticated varieties known to belong to the same species, they are here available as evidence of what may be termed racial incompatibility, or of the particular kind of variation which my theory requires. To quote only two instances: "The yellow and white varieties (of Verbascum) when crossed produce less seed than the similarly coloured varieties"; and the blue and red varieties of the pimpernel are absolutely sterile together, while each is perfectly fertile within itself. Such instances are the more suggestive on account of their arising under domestication, because, as a rule, domestication increases fertility, and is thus inimical to sterility—sometimes even breaking down the physiological barriers between natural species. Therefore, if in some cases even under domestication the reproductive system may vary in this manner, so as to erect physiological barriers between artificial varieties, much more are such barriers likely to be erected between varieties when these arise in a state of nature.

But as regards varieties in a state of nature, I have not been able to meet with any evidence of racial incompatibility. Nor is this to be wondered at: for, unless the degree of such incompatibility were well pronounced, it would not be noticed; while, if it were well pronounced, the two varieties would for this very reason be classified as species. Therefore, the fact of racial incompatibility within the limits of wild species could only be proved by experiments undertaken expressly for the purpose, in the way which I shall afterwards explain.

(3) *Species.*—According to the general theory of evolution, which in this paper is taken for granted, the distinction between varieties and species is only a distinction of degree; and the distinction is mainly, as well as most generally, that of mutual sterility. Therefore my theory of physiological selection is here furnished with an incalculable number of instances of the particular kind of variation which is required; for in so many instances as variation has led to any degree of sterility between parent and varietal forms—or between the varying descendants of the same form—in so many instances it is merely a statement of fact to say that physiological selection must have taken place. There remains, however, the question whether the particular change in the reproductive system which led to all these cases of mutual sterility was anterior or posterior to changes in other parts of the organism. For, if it was anterior, these other changes—even though they be adaptive changes—were presumably due to the sexual change having interposed its barrier to crossing with parent forms; while, if the sexual change were posterior to the others, the presumption would be that it was the latter which, by their reaction on the sexual system, induced the former. I shall have to consider this alternative later on. Here, therefore, it is enough to point out that under either possibility the principles of physiological selection must have been at work; only these principles are accredited with so much the more causal influence in the production of species in the proportion that we find reason to suppose the sexual change to have been, as a rule, the prior change. But under either alternative, and on the doctrine that species are extreme

varieties, we have many hundreds of thousands of instances of fertility within the varietal forms with sterility towards allied forms.

Probably enough has now been said to show that, as a matter of fact, the particular kind of variation in the reproductive system which is required by the theory of physiological selection does occur, firstly, in individuals; secondly, in races; and thirdly, in species. But the evidence of physiological selection as an agency in the evolution of species is so far only *primâ facie*. That is to say, although we have evidence to prove the occurrence of this particular kind of variation, and although we can see that whenever it does occur it must be preserved, as yet we have seen no evidence to show how far this kind of variation has been at work in the formation of species. I will, therefore, next proceed to give an outline sketch of the evidence which I have been able to find, tending to show that the facts of organic nature are such as they ought to be, if it is true that physiological selection has played any considerable part in their causation. And to do this I will begin by taking the three cardinal objections to the theory of natural selection with which I set out—namely, sterility, intercrossing, and inutility. For, as we shall see—and this in itself is a suggestive consideration—all the facts which here present formidable obstacles to the theory of natural selection, when this is regarded only as a theory of the origin of species, are not only explained by the theory of physiological selection, but furnish to that theory some of the best evidence which I have been able to find.

Argument from Sterility.—In what respects do species differ from one another? They differ firstly, chiefly, and most generally in respect of their reproductive systems: this, therefore, I will call the primary difference. Next, they differ in an endless variety of more or less minute details of structure, which are sometimes adaptive and sometimes not. These, therefore, I will call the secondary differences. Now, the secondary differences are never numerous as between any two allied species: in almost all cases they admit of being represented by units. Yet, if it were possible to enumerate all the specific differences throughout both the vegetable and animal kingdoms, there would be required a row of figures expressive of many millions. In other words, the secondary specific distinctions may occur in any parts of organisms, but never occur in many parts of the same organism. So that, if we have regard to the whole range of species, the secondary distinctions are seen to be, in the highest imaginable degree, variable or inconstant: the only distinction which is at all constant or general is the primary distinction, or the one which belongs exclusively to the reproductive system. Surely, therefore, what we primarily require in any theory of the origin of *species*, is an explanation of this relatively constant or general distinction. But this is just what all previous theories fail to supply. Natural selection accounts for some among the many secondary distinctions, but is confessedly unable to explain the primary distinction. The same remark applies to sexual selection, use and disuse, economy of growth, correlated variability, and so forth. Even the prevention of intercrossing by geographical barriers or by migration is unable to explain the very general occurrence of some degree of sterility between two allied varieties which have diverged sufficiently to take rank as different species. All these theories, therefore, are here in the same predicament: they profess to be theories of the origin of species, and yet none of them is able to explain the one fact which more than any other goes to constitute the distinction between species and species. The consequence is that most evolutionists here fall back upon a great assumption: they say it must be the change of organisation which causes the sterility—it must be the secondary distinctions which determine the primary. But the contrary proposition is surely at least as probable, namely, that it is the sterility which, by preventing intercrossing with parent forms, has determined the secondary distinctions—or, rather, that it has been the original condition to the operation of the modifying causes in all cases where free intercrossing has not been otherwise prevented. For, obviously, it is a pure assumption to say that the secondary differences have always been historically prior to the primary difference, and that they stand to it in the relation of cause to effect. Moreover, the assumption does not stand the test of examination, as I will now proceed to show.

(1) On merely *a priori* grounds it scarcely seems probable that whenever any part of any organism is slightly changed in any way by natural selection, or by any other cause, the reproductive system should forthwith respond to that change by becoming sterile with allied forms. Yet this is really what the assumption in question requires, seeing that *all* parts of organisms are subject to the secondary specific distinctions. What we find in nature is a more or less constant association between the one primary distinction and an endless profusion of secondary distinctions. Now, if this association had been between the primary distinction and some one—or even some few—secondary distinctions, constantly the same in kind; in this case I could have seen that the question would have been an open one as to which was the conditional and which the conditioned. But as the case actually stands, on merely antecedent grounds, it does not appear to me that the question is an open one. Here we have a constant peculiarity of the reproductive system, repeated over and over again—millions of times—throughout organic nature; and we perpetually find that when this peculiar condition of the reproductive system is present, it is associated with structural changes elsewhere, which, however, may affect any part of any organism, and this in any degree. Now, I ask, is it a reasonable view that the one constant peculiarity is always the result, and never the condition, of any among these millions of inconstant and organically minute changes with which it is found associated?

(2) But, quitting *a priori* grounds, it is a matter of notorious fact that in the case of nearly all our innumerable artificial productions, organisms do admit of being profoundly changed in a great variety of ways, without any reaction on the reproductive system following as a consequence.

(3) Again, as regards wild species, Mr. Darwin proves that "the correspondence between systematic affinity and the facility of crossing is by no means strict. A multitude of cases could be given of very closely allied species which will not unite, or only with extreme difficulty; and, on the other hand, of very distinct species which unite with the utmost facility." And he goes on to say that "within the limits of the same family, or even of the same genus, these opposite cases may occur"; so that "the capacity of the species to cross is often completely independent of this systematic affinity, that is, of any difference in their structure or constitution, excepting in their reproductive systems." Now, on the supposition that sterility between species is always, or generally, caused by the indirect influence on the reproductive system of changes taking place in other parts of the organism, these facts are unintelligible—being, indeed, as a mere matter of logic, contradictory of the supposition.

(4) Mr. Darwin further shows that, "independently of the question of fertility, in all other respects there is the closest general resemblance between hybrids and mongrels." Clearly, this fact implies that natural selection and artificial selection run perfectly parallel in all other respects, save in the one respect of reacting on the reproductive system, where, according to the views against which I am arguing, they must be regarded as differing, not only constantly, but also profoundly.

(5) Lastly, Mr. Darwin concedes—or rather insists—

that "the primary cause of the sterility of crossed species is confined to differences in their sexual elements." A general fact which assuredly proves that the primary specific distinction is one with which the organism as a whole is not concerned: it is merely a local variation which is concerned only with the sexual system. Why, then, should we suppose that it differs from a local variation taking place in any other part of the organism? Why should we suppose that, unlike all other such variations, it can never be independent, but must always be superinduced as a secondary result of changes taking place elsewhere? It appears to me that the only reason why evolutionists suppose this is because the particular variation in question happens to have as its result the origination of species; and that, being already committed to a belief in natural selection or other agencies as the causes of such origination, they are led to regard this particular kind of local variation as not independent, but superinduced as a secondary result of these other agencies operating on other parts of the organism. But once let evolutionists clearly perceive that natural selection is concerned with the origin of species only in so far as it is concerned with the origin of adaptive structures—or of some among the secondary distinctions—and they will perceive that the primary specific distinction takes its place beside all other variations as a variation of a local character, which may, indeed, at times be due to the indirect influence of natural selection, use, disuse, and so forth; but which may also be due to any of the numberless and hidden causes that are concerned with variation in general.[1]

I trust, then, that reasons enough have now been given to justify my view that, if we take a broad survey of all the facts bearing on the question, it becomes almost impossible to doubt that the primary specific distinction is, as a general rule, the primordial distinction. I say "as a general rule," because the next point which I wish to present is that it constitutes no part of my argument to deny that in some—and possibly in many—cases the primary distinction may have been superinduced by the secondary distinctions. Indeed, looking to the occasional appearance of partial sterility between our domesticated productions, as well as to the universally high degree of it between genera, and its universally absolute degree between families, orders, and classes, I see the best of reasons to conclude that in *some* cases the sterility between *species* may have been originally caused, *and in a much greater number of cases subsequently intensified*, by changes going on in other parts of the organism. Moreover, I doubt not that of the agencies determining such changes natural selection is probably one of the most important. But what does this amount to? It amounts to nothing more than a re-statement of the theory of physiological selection. It merely suggests hypothetically the cause, or causes, of that particular variation in the reproductive system with which alone the theory of physiological selection is concerned, and which, as a matter of fact, *howsoever caused*, is found to constitute the one cardinal distinction between species and species. Therefore I am really not concerned with what I deem the impossible task of showing how far, or how often, natural selection—or any other cause—may have induced this particular kind of variation in the reproductive system by its operations on other parts of an organism. Even if I were to go the full length that other evolutionists have gone, and regard this primary specific distinction as in all cases due to the secondary specific distinctions, still I should not be vacating my theory of physiological selection: I should merely be limiting the possibilities of variation within the reproductive system in what I now consider a wholly unjustifiable manner. For, as previously stated, it appears to me much the more rational view that the primary specific distinction is likewise, as a rule, the primordial distinction; and that the cases where it has been superinduced by the secondary distinctions are comparatively few in number.[1]

If we thus regard sterility between species as the result of what I have called a local variation, or a variation arising only in the reproductive system—whether this be induced by changes taking place in other parts of the organism, to changes in the conditions of life, or to changes inherent in the reproductive system itself—we can understand why such sterility rarely, though sometimes, occurs in our domesticated productions; why it so generally occurs in some degree between species; and why as between species it occurs in all degrees.

It rarely occurs in our domesticated productions because it has never been the object of breeders or horticulturists to preserve this kind of variation. Yet it sometimes does occur in some degree among our domesticated productions, because the changes produced on other parts of the organism by artificial selection do, in a small percentage of cases, react upon the reproductive system in the way of tending to induce sterility with the parent form, while not lessening fertility with the varietal form. Again, this particular condition of the reproductive system is so generally characteristic of species simply because in as many cases as it occurs it has constituted the reason why species exist as species. And, lastly, this particular variation in the reproductive system has taken place under nature in such a variety of degrees—from absolute sterility between species up to complete, or even to more than complete, fertility—because natural species, while being records of this particular *kind* of variation are likewise the records of all *degrees* of such variation which have proved sufficient to prevent overwhelming intercrossing with parent forms. Sometimes this degree has been less than at other times, because other conditions—climatic, geographical, habitatorial, physiological, and even psychological[2]—have co-operated to prevent intercrossing, with the result of a correspondingly less degree of sterility being required to secure a differentiation of specific type. Lastly, where species have been evolved on different geographical areas, or by use, disuse, and other causes of a similarly "direct" kind, there has been no need to prevent intercrossing in any degree; so that allied species formed under any of these conditions may still remain perfectly fertile, or even more than naturally fertile, with one another.

In view of these considerations, I should regard it as a serious objection to my theory if it could be shown that sterility between allied species is invariably absolute, or even if it could be shown that there are no cases of unimpaired fertility. What my theory would expect to find is exactly what we do find—namely, an enormous majority

[1] Mr. Darwin himself does not appear to have held the view against which I am now arguing—viz. that the primary distinction is always, or usually, superinduced by the secondary. Not even here, therefore, is his authority opposed to my views: upon this question his voice is merely silent.

[1] The paper here develops another line of argument which it is difficult to render in abstract. Its object, however, is to show that, even in the cases where the primary distinction is superinduced by the secondary—whether these cases are, as I believe, "comparatively few" or comparatively numerous—my theory is available to explain why the primary distinction is so habitual an accompaniment of the secondary distinctions, of whatever kinds or degrees the latter may happen to be. For, according to my theory, the reason of this association in such cases is that it can only be those kinds and degrees of secondary distinction which are able so to react on the reproductive system as to induce the primary distinction that are, *for this reason*, preserved. Or, otherwise expressed, in cases where the secondary distinctions induce the primary, the former owe their existence to the fact that they happened to be of a kind capable of producing this particular effect. Under this view, even in these cases it is the principles of physiological selection that have determined the kinds of secondary distinction which are allowed to survive. For 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—a general view of the subject which appears to be justified by the very general association between the two.

[2] See "Origin of Species," p. 81, where it is shown that among vertebrated animals different varieties of the same species, even when living on the same area, frequently exhibit a marked repugnance to pairing with one another. In the same passage, it is remarked the different varieties sometimes occupy different stations.

of instances where sterility occurs in all degrees, with a few exceptional instances where secondary distinctions have been able to develop without being associated with the primary distinction. So that, on the whole, I cannot but candidly consider that all the facts relating to the sterility of natural species are just what they ought to be, if they have been in chief part due to the principle which I am advocating. Mr. Darwin appears to have clearly perceived that there must be some one principle serving to explain all these facts—so curiously related, and yet so curiously diverse. For he says, and he says most truly, "We have conclusive evidence that the sterility of species must be due to some principle quite independent of natural selection." I trust I have now said enough to show that, in all probability, this hitherto undetected principle is the principle of physiological selection.

(*To be continued.*)

PHYSIOLOGICAL SELECTION: AN ADDITIONAL SUGGESTION ON THE ORIGIN OF SPECIES[1]

III.

ARGUMENT from the Prevention of Intercrossing.—This argument is the same from whatever cause the prevention of intercrossing may arise. Where intercrossing is prevented by geographical barriers or by migration, it is more easy to prove the evolution of new species as a consequence than it is when intercrossing is prevented by physiological barriers; for in the latter case the older and the newer forms will probably continue to occupy the same area, and then there will be no independent evidence to show that the severance between them was due to the prevention of intercrossing. Nevertheless, all the evidence I have of the large part that geographical barriers have played in the evolution of species by preventing intercrossing with parent forms goes to show the probable importance of physiological barriers when acting in the same way. Hence it will be better to postpone this line of argument in favour of physiological selection until the appearance of my next paper, where I shall hope to show, from evidence furnished by the geographical distribution of species, how predominant a part the prevention of intercrossing has played in the evolution of species. Here, therefore, I will merely remark that wherever intercrossing with parent forms is prevented, in the proportion that it is prevented a better opportunity is given to natural selection for seizing upon any beneficial variations that may happen to arise. On this account physiological selection probably lends important aid to natural selection, thus becoming indirectly instrumental in the evolution of useful as well as of useless structures.

There is also another respect in which these two kinds of selection probably co-operate. For Mr. Darwin shows that "it would be clearly advantageous to two varieties, or incipient species, if they could be kept from blending, on the same principle that, when man is selecting at the same time two varieties, it is necessary that he should keep them separate." But he proceeds to show that this advantage cannot be conferred by natural selection, and hence that the sterility which is so generally characteristic of species cannot be attributed to this agency. We have, however, just seen that this sterility is in all likelihood due to physiological selection; and therefore, if it be true, as Mr. Darwin thought, that "it would profit an incipient species if it were rendered in some slight degree sterile with its parent form," physiological selection and natural selection may mutually assist one another. For, although the benefit of this sterility could not have been initially conferred by natural selection, yet when it once arises from an independent variation in the reproductive system, there is no reason why it should not forthwith be favoured by natural selection, just as is the case with advantageous variations in general.

[1] Abstract of a Paper read before the Linnean Society on May 6, by George J. Romanes, M.A., LL.D., F.R.S. &c. Continued from p. 340.

Feeling how grave a difficulty was presented to his theory of the origin of species by the general sterility of species, Mr. Darwin was extremely anxious to find some way in which natural selection might be seen to have brought about this result. Had it occurred to him that this result was probably nothing more than the necessary expression of a particular kind of variation on the part of the reproductive system, I cannot doubt that he would have felt the theory of natural selection to have been relieved of one of its greatest disabilities.

Argument from the Inutility of Specific Differences.—After what has already been said on this subject, I will here only deal with one question, namely, Why is it that apparently useless structures occur in such profusion among species, in much less profusion among genera, and scarcely at all among families, orders, and classes? It may be answered that the points wherein species differ from species are usually points of smaller detail than those which distinguish genera, families, &c., and thus may well actually be as a rule less useful, although still not absolutely useless: natural selection, it may be urged, is better able than is the naturalist to diagnose utility. But here again we have a most unwarranted appeal to the argument from ignorance; whereas, according to my view, it is quite intelligible that when a varietal form is differentiated from its parent form by the bar of sterility, isolation, or migration, any little meaningless peculiarities of structure (or of instinct[1]) should at first be allowed to arise, but should eventually be eliminated as so much surplusage in the struggle for existence, by economy of growth, or even by independent variation when undirected by natural selection. A greater or less time would in different cases be required to effect this reduction, and thus we can understand why they are sometimes allowed to persist into genera, but rarely into families.

Again, if apparently useless specific characters (whether these be new structures or modifications of old ones, slight changes in form, colour, and so forth) are thus regarded as really useless, we should expect that they ought to be of a kind which do not impose much physiological tax upon the organism, since otherwise natural selection would not have allowed them to become so much as specific characters. Well, I have applied this test, and find it is a most general rule that specific characters the utility of which cannot be perceived are such as do not impose any considerable demand for nourishment: either on account of their small size or of their organically inexpensive material, they do not impose much tax upon the organism. Now it is obvious that there can be no connection between utility as disguised and smallness of size or inexpensiveness of material; while it is no less obvious that there is a close connection between these things and a real inutility.

Lastly, our domesticated varieties occasionally exhibit well-marked and more or less constant characters of a useless kind. Here there can scarcely be any question about the genuineness of the inutility, seeing that the characters have arisen only under domestication, or in the absence of any struggle for existence. Yet these structures are sometimes of the most curious and complex morphology—even more so than innumerable apparently useless structures in the case of natural species.[2]

Argument from Divergence of Character.—Any theory of the origin of species in the way of descent must be prepared with an answer to the question, Why have species *multiplied?* Why have they not simply become transmuted in linear series instead of ramifying into branches? This question Mr. Darwin seeks to answer

[1] For instances of useless instincts see Mr. Darwin's posthumous essay published in my "Mental Evolution in Animals." It is suggestive in the present connection that, just like useless structures, useless instincts, so far as I can find, only occur in species and genera: never in families, orders, or classes.

[2] For a good instance of this see "Variation of Plants and Animals under Domestication," vol. i. pp. 78-79.

"from the simple circumstance that the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the economy of nature, and so be enabled to increase in numbers."[1] And he proceeds to illustrate this principle by means of a diagram, showing the hypothetical divergence of character undergone by the descendants of seven species. Thus, he attributes divergence of character exclusively to the influence of natural selection.

Now, this argument appears to me unassailable in all save one particular; but this is a most important particular: the argument wholly ignores the effect of intercrossing with parent forms. Granting to the argument that intercrossing with parent forms is prohibited, and nothing can be more satisfactory. The argument, however, sets out with showing that it is in limited areas, or in areas already overstocked with the specific forms in question, that the advantages to be derived from diversification will be most pronounced. Or, in Mr. Darwin's words, it is where they "jostle each other most closely" that natural selection will set a premium upon any members of the species which may depart from the common type. Now, inasmuch as this jostling or overcrowding of individuals is a needful condition to the agency of natural selection in the way of diversifying character, must we not feel that the general difficulty from intercrossing previously considered is here presented in a special and aggravated form? At all events, I know that, after having duly and impartially considered the matter, to me it does appear that, unless the swamping effects of intercrossing with the parent form on an overcrowded area is in some way prevented to begin with, natural selection could never have any material supplied by which to go on with. Let it be observed that I regard Mr. Darwin's argument as perfectly sound where it treats of the divergence of *species* from one another—*i.e.* of the rise of genera, families, &c.; for then physiological barriers are present to prevent intercrossing. But in applying the argument to explain the divergence of *individuals* into *varieties* it seems to me that here, more than anywhere else, he has lost sight of the formidable difficulty in question. For in this particular case so formidable does the difficulty seem to me, that I cannot believe natural selection alone could produce any divergence of character so long as all the individuals on an overcrowded area occupy that area together. Yet if any of them quit that area, and so escape from the unifying influence of free intercrossing, these individuals also escape from the conditions which Mr. Darwin names as those that are needed by natural selection in order to produce divergence. Therefore it appears to me that, under the circumstances supposed, natural selection alone could not produce divergence; the most it could do would be to change the whole specific type in some one direction (the needful variations in that one direction being caused by some general change of food, climate, habit, &c., affecting a number of individuals simultaneously), and thus induce transmutation of species in a linear series—each succeeding member of which might supplant its parent form. But, in order to secure diversity, multiplication, or ramification of species, it appears to me obvious that the primary condition required is that of preventing intercrossing with parent forms at the origin of each branch—whether the prevention be from the first absolute, or only partial. And, after all that has been previously said, it is needless again to show that the principles of physiological selection are at once the only principles which are here likely to be efficient, and the principles which are fully capable of doing all that is required. For species, as they now stand, unquestionably prove the fact of ramification; and it appears to me no less unquestionable that ramification, as often as it has occurred, can only have been permitted to occur by the absence of intercrossing with parent forms. But apart from geographical barriers (which, according to Mr. Darwin's argument, would be inimical to the divergence of character by natural selection), the ramification can only take place as a consequence of physiological selection, or as a consequence of some change in the reproductive system which prevents intercrossing with unchanged (or differently changed) compatriots. But when once this condition is supplied by physiological selection, I have no doubt that divergence of character may then be promoted by natural selection, in the way that is explained by Mr. Darwin.

From which it will be seen that the theory of physiological selection has this advantage over the theory of natural selection in the way of explaining what Mr. Darwin calls diversification of character, or what I have called the ramification of species. This diversification or ramification has reference chiefly to the secondary specific distinctions, which, as we have seen, the theory of natural selection supposes to be the first changes that occur, and, by their occurrence, to induce the primary distinction of sterility. My theory, on the other hand, inverts this order, and supposes the primary distinction to be likewise (in most cases) the primordial distinction. Now, the advantages thus gained are twofold. In the first place, as just shown, we are able to release the principle of natural selection from what appears to me the otherwise hopeless difficulty of effecting diversification of character on an overcrowded area with nothing to prevent free intercrossing. And, in the next place, as we can now see, we are able to find an additional reason for the diversification of character, over and above the one that is relied upon by Mr. Darwin. For, by regarding the primary distinction of sterility as likewise the primordial distinction, we are able to apply to an incipient variety, inhabiting even an overcrowded area, the same principles which are known to lead to diversification by geographical barriers or by migration, as previously explained. In other words, if once we regard the primary distinction of sterility as also the initial distinction, instead of the incidental result of secondary distinctions, Mr. Darwin's argument touching the causes of diversification is not merely saved: it is notably extended by the addition of an independent principle, which, as we know from other evidence, is a principle of high importance in this respect.

Argument from Geographical Distribution.—The body of evidence under this head is too large to be given in an abstract; but the following are some of the chief points.

Mr. Darwin took a great deal of trouble to collect evidence on the two following facts, namely, (1) that "species of the larger genera in each country vary more frequently than the species of smaller genera"; and (2) that "many of the species included within the larger genera resemble varieties in being very closely, but unequally, related to each other." By larger genera he means genera containing many species, and he accounts for these general facts by the principle "that where many species of a genus have been formed, on an average many are still forming." But how forming? If we say by natural selection alone, we should expect to find the multitudinous species differing from one another in respect of features presenting utilitarian significance; yet this is precisely what we do not find. For Mr. Darwin's argument here consists in showing that "in large genera the amount of difference between the species is often exceedingly small, so that in this respect the species of the larger genera resemble varieties more than do the species of the smaller genera." Therefore the argument, while undoubtedly a very forcible one in favour of the fact of *evolution*, appears to me scarcely consistent with the theory of *natural selection*. On the other hand, the argument tells strongly (though unconsciously) in favour

[1] "Origin of Species," p. 87.

of physiological selection. For, the larger a genus, or the greater number of species it contains, the greater must be the opportunity afforded for the occurrence of that particular kind of variation on which the principle of physiological selection depends. All the species of a genus may be regarded as so many varieties which have already been separated from one another physiologically: therefore each of them may now constitute a new starting-point for a further and similar separation—particularly as, in virtue of their previous segregation, many of them are now exposed to different conditions of life. Thus, it seems to me, we can well understand why it is that genera already rich in species tend to grow still richer; while such is not the case in so great a degree with genera that are poor in species. Moreover, we can well understand that, multiplication of species being in the first instance determined by changes in the reproductive system alone, wherever a large number of new species are being turned out, the secondary differences between them should be "often exceedingly small"—a general correlation which, so far as I can see, we are not able to understand on the theory of natural selection.

Another general fact mentioned by Darwin, and now well recognised by all naturalists, is that closely allied species, or species differing from one another in trivial details, usually occupy contiguous areas; or, conversely stated, that contiguity of geographical position is favourable to the appearance of species closely allied to one another. Of course this fact speaks in favour of evolution; but where the question is as to method, I confess that the theory of natural selection appears to me wholly irrelevant. For, in most of the numberless cases to which I allude, the points of minute detail wherein the allied species differ in respect of secondary distinctions, are points which present no utilitarian significance. And, as previously argued, it is impossible to believe that there can be any general or constant correlation between disguised utility and insignificance of secondary distinction.

Now the large body of facts to which I here allude, but which I have not space to detail, appears to me to constitute perhaps the strongest of all my arguments in favour of physiological selection. Take, for instance, a large continental area, and follow across it a chain of species, each link of which differs from those on either side of it by the most minute and trivial distinctions of a secondary kind; but all the links of which differ from one another in respect of their reproductive systems, so that no one member of the series is perfectly fertile with any other member. Can it be supposed that in every case this constant primary distinction has been superinduced by the trivial secondary distinctions, distributed as they are over different parts of all these kindred organisms, and yet nowhere presenting any but the most trifling amount of morphological change? Or, even if we were to suppose this, we have still to meet the question, How were all these trifling changes produced in the face of free intercrossing on the continental area? Certainly not by natural selection, seeing that they are all useless to the species presenting them. Let it then be by changes in the conditions of life, whether of food, of climate, or of anything else. I can conceive of no other alternative. Yet, if we accept this alternative, we are but espousing—in a disguised and roundabout way, to be sure—the theory of physiological selection. For we are thus but hypothetically assigning the causes which have induced the primary distinction in each case, or the causes which have led to the mutual sterility. For my own part, I believe that the assignation would be, in the great majority of such cases, incorrect. That is to say, I do not believe that in the great majority of such cases the trivial secondary distinctions—however these were caused—can have had anything to do with the great primary distinction. What I believe is that all the closely-allied species inhabiting our supposed continent, and differing from one another in so many points of minute detail, are but so many records of one particular kind of variation having taken place in the reproductive systems of their ancestors, and which, so often as it did take place, necessarily gave birth to a new species. The primary distinction thus became the constant distinction, simply because it was in virtue of this distinction—or in virtue of the variation which first originated this distinction—that the species became species; and the secondary distinctions thus became multitudinous, minute, and unmeaning, simply because they were of later origin, the result of spontaneous variability, unchecked by intercrossing with the parent forms, and, on account of their trivial (*i.e.* physiologically harmless) nature, unchecked also by natural selection, economy of growth, or any other principle which might have prevented spontaneous variability of any other kind.

There are many other general facts relating to geographical distribution which lend the strongest countenance to the theory of physiological selection—in particular I may mention the difficulty which Mr. Darwin experiences in accounting for the absence or rarity of transitional varieties between species inhabiting contiguous areas (*loc. cit.*, p. 134), which is just what might have been expected on my theory—but it is time that this abstract should draw to a close.

Relations between the Theories of Natural Selection and Physiological Selection.—The two theories resemble one another in the kind of evidence by which they are each supported. For in neither case is this evidence that of direct observation of the transmutation of species under the influence of the agency supposed: the evidence in each case consists in first proving the facts on which the principle depends, and then showing that the phenomena of organic nature are such as they ought to be if the principle in question has had any large share in their production. But the two theories differ in that while natural selection is a theory of the origin of genera, families, orders, and classes even more than it is of the origin of species; the theory of physiological selection is almost exclusively a theory of the origin of species. Again, the latter theory differs from the former in that the variations on the occurrence of which it depends are variations of a comparatively unuseful, or non-adaptive, kind. Nevertheless, physiological selection must be quite as vigilant as natural selection, and it seizes upon the comparatively unuseful variation of sterility with even more certainty than natural selection can seize upon any useful variation. Lastly, as will have been gathered from the foregoing abstract, the two theories are in no way opposed to one another: they are, in fact, complementary, and the principles with which they have to deal co-operative. For, on the one hand, without the assistance of physiological selection, natural selection would, I believe, be all but overcome by the adverse influences of free intercrossing—influences all the more potent under the very conditions which are required for the multiplication of species by divergence of character. On the other hand, without natural selection, physiological selection would be powerless to create any differences of specific type other than those of mutual sterility and trivial details of structure, form, or colour—differences wholly without meaning from a utilitarian point of view. But in their combination these two principles appear to me able to accomplish what neither can accomplish alone—namely, a full and satisfactory explanation of the origin of species.

Conclusion.—It has not been possible to do justice to the theory of physiological selection within the limits of this abstract. But perhaps enough has been said to show that there is a great deal of evidence in its support; that by regarding mutually sterile species as records of variation in reproductive systems, we are at work, so to speak, on the foundation of the matter; and that we are thus able to explain a number of general facts which do not

admit of being explained by any previous theory. It only remains to add that, if true, the present theory ought to admit of experimental verification. Let well-marked natural varieties of plants growing on the same area be systematically tested with regard to their relative *degrees* of fertility, first within themselves, and next towards one another: let these experiments be made in successive years over a number of natural varieties, by carefully-conducted artificial fertilisation, and by counting the seeds and tabulating the results. In this way experimental evidence would probably be obtained of degrees of sterility between even slight though constant varieties growing on the same areas; and, if so, such evidence would serve as further proof of the present theory. But experiments of this kind, in order to be satisfactory, ought to be conducted by a number of observers in different geographical areas; and my object in publishing so lengthy an abstract of my views in this periodical is that of inducing naturalists in other parts of the world to co-operate with me in carrying out this research. The paper itself, which furnishes fuller particulars as to the way in which such experiments should be carried out, is published in a separate form by the Linnean Society.