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DARWIN, AND AFTER DARWIN

III

POST-DARWINIAN QUESTIONS
ISOLATION AND PHYSIOLOGICAL SELECTION

BY THE SAME AUTHOR.

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DARWIN, AND AFTER DARWIN

AN EXPOSITION OF THE DARWINIAN THEORY
AND A DISCUSSION OF
POST-DARWINIAN QUESTIONS

BY THE LATE
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Honorary Fellow of Gonville and Caius College, Cambridge

III
POST-DARWINIAN QUESTIONS
ISOLATION
AND PHYSIOLOGICAL SELECTION

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PREFACE

Of the six chapters which constitute this concluding volume of G. J. Romanes' *Darwin, and after Darwin*, three, the first two and the last, were in type at the time of his death. I have not considered myself at liberty to make any alterations of moment in these chapters. For the selection and arrangement of all that is contained in the other three chapters I am wholly responsible.

Two long controversial Appendices have been omitted. Those marked A and B remain in accordance with the author's expressed injunctions. In a third, marked C, a few passages from the author's note-books or MSS. have been printed.

The portrait of the Rev. J. Gulick, which forms the frontispiece, was prepared for this volume before the author's death. Mr. Gulick's chief contributions to the theory of physiological selection are to be found in the Linnean Society's *Journal* (*Zoology*, vols. xx and xxiii), and in four letters to *Nature* (vol. xli. p. 536; vol. xlii. pp. 28 and 369; and vol. xliv. p. 29). [Pg vi]

I have to thank Mr. Francis Galton, D.C.L., F.R.S. and Mr. F. Howard Collins for valuable assistance generously rendered for the sake of one whom all who knew him held dear. For he was, if I may echo the words of Huxley, "a friend endeared to me, as to so many others, by his kindly nature, and justly valued by all his colleagues for his powers of investigation and his zeal for the advancement of science."

C. Lloyd Morgan.

Bristol, *May 1897*.

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ISOLATION

[Pg 1]

CHAPTER I.
Isolation.

This treatise will now draw to a close by considering what, in my opinion, is one of the most important principles that are concerned in the process of organic evolution—namely, Isolation. I say in *my* opinion such is the case, because, although the importance of isolation is more or less recognized by every naturalist, I know of only one other who has perceived all that the principle involves. This naturalist is the Rev. J. Gulick, and to his essays on the subject I attribute a higher value than to any other work in the field of Darwinian thought since the date of Darwin's death[1].

For it is now my matured conviction that a new point of departure has here been taken in the philosophy of Darwinism, and one which opens up new territories for scientific exploration of an endlessly wide and varied character. Indeed I believe, with Mr. Gulick, that in the principle of [Pg 2] Isolation we have a principle so fundamental and so universal, that even the great principle of Natural Selection lies less deep, and pervades a region of smaller extent. Equalled only in its importance by the two basal principles of Heredity and Variation, this principle of Isolation constitutes the third pillar of a tripod on which is reared the whole superstructure of organic evolution.

By isolation I mean simply the prevention of intercrossing between a separated section of a species or kind and the rest of that species or kind. Whether such a separation be due to geographical barriers, to migration, or to any other state of matters leading to exclusive breeding within the separated group, I shall indifferently employ the term isolation for the purpose of designating what in all cases is the same result—namely, a prevention of intercrossing between A and B, where A is the separated portion and B the rest of the species or kind.

The importance of isolation as against dissimilar forms has always been fully appreciated by breeders, fanciers, horticulturists, &c., who are therefore most careful to prevent their pedigree productions from intercrossing with any other stock. Isolation is indeed, as Darwin has observed, "the corner-stone of the breeder's art." And similarly with plants and animals in a state of nature: unless intercrossing with allied (i.e. dissimilar) forms is prevented, the principle of heredity is bound to work for uniformity, by blending the dissimilar types in one: only when there is exclusive breeding of similarly modified forms can the principle of heredity work in the direction of change—i.e. of evolution.

Now, the forms of isolation—or the conditions which may lead to exclusive breeding—are [Pg 3] manifold. One of the most important, as well as the most obvious, is geographical isolation; and no one questions that this has been an important factor in the process of evolution, although opinions still vary greatly as to the degree of its importance in this respect. At one end of the series we may place the opinion of Mr. Wallace, who denies that any of what may be termed the evolutionary effect of geographical isolation is due to "influence exerted by isolation *per se*." This effect, he says, is to be ascribed exclusively to the fact that a geographically isolated portion of a species must always encounter a change of environment, and therefore a new set of conditions necessitating a new set of adaptations at the hands of natural selection[2]. At the other end of the series we must place the opinion of Moritz Wagner, who many years ago published a masterly essay[3], the object of which was to prove that, in the absence of geographical isolation (including migration), natural selection would be powerless to effect any change of specific type. For, he argued, the initial variations on which the action of this principle depends would otherwise be inevitably swamped by free intercrossing. Wagner adduced a large number of interesting facts in support of this opinion; but although he thus succeeded in enforcing the truth that geographical isolation is an important aid to organic evolution, he failed to establish his conclusion that it is an indispensable condition. Nevertheless he may have been right—and, as I shall presently show, I [Pg 4] believe he was right—in his fundamental premiss, that in the presence of free intercrossing natural selection would be powerless to effect divergent evolution. Where he went wrong was in not perceiving that geographical isolation is not the only form of isolation. Had it occurred to him that there may be other forms quite as effectual for the prevention of free intercrossing, his essay could hardly have failed to mark an epoch in the history of Darwinism. But, on account of this oversight, he really weakened his main contention, namely, that in the presence of free intercrossing natural selection must be powerless to effect divergent evolution. This main contention I am now about to re-argue. At present, therefore, we have only to observe that Wagner did it much more harm than good by neglecting to perceive that free intercrossing may be prevented in many other ways besides by migration, and by the intervention of geographical barriers.

In order that we may set out with clearer views upon this matter, I will make one or two preliminary remarks on the more general facts of isolation as these are found to occur in nature.

In the first place, it is obvious that isolation admits of degrees: it may be either total or partial; and, if partial, may occur in numberless grades of efficiency. This is so manifest that I need not wait to give illustrations. But now, in the second place, there is another general fact appertaining to isolation which is not so manifest, and a clear appreciation of which is so essential to any adequate consideration of the subject, that I believe the reason why evolutionists have hitherto [Pg 5] failed to perceive the full importance of isolation, is because they have failed to perceive the distinction which has now to be pointed out. The distinction is, that isolation may be either discriminate or indiscriminate. If it be discriminate, the isolation has reference to the resemblance of the separated individuals to one another; if it be indiscriminate, it has no such reference. For example, if a shepherd divides a flock of sheep without regard to their characters, he is isolating one section from the other indiscriminately; but if he places all the white sheep in one field, and all the black sheep in another field, he is isolating one section from the other discriminately. Or, if geological subsidence divides a species into two parts, the isolation will be indiscriminate; but if the separation be due to one of the sections developing, for example, a change of instinct determining migration to another area, or occupation of a different habitat on the same area, then the isolation will be discriminate, so far as the resemblance of instinct is concerned.

With the exception of Mr. Gulick, I cannot find that any other writer has hitherto stated this

supremely important distinction between isolation as discriminate and indiscriminate. But he has fully as well as independently stated it, and shown in a masterly way its far-reaching consequences. Indiscriminate isolation he calls Separate Breeding, while discriminate isolation he calls Segregate Breeding. For the sake, however, of securing more descriptive terms, I will coin the words Apogamy and Homogamy. Apogamy, of course, answers to indiscriminate isolation, or separate breeding. Homogamy, on the other hand, answers to discriminate isolation, [Pg 6] or segregate breeding: only individuals belonging to the same variety or kind are allowed to propagate. Isolation, then, is a genus, of which Apogamy and Homogamy are species[4].

Now, in order to appreciate the unsurpassed importance of isolation as one of the three basal principles of organic evolution, let us begin by considering the discriminate species of it, or Homogamy.

To state the case in the most general terms, we may say that if the other two basal principles are given in heredity and variability, the whole theory of organic evolution becomes neither more nor less than a theory of homogamy—that is, a theory of the causes which lead to discriminate isolation, or the breeding of like with like to the exclusion of unlike. For the more we believe in heredity and variability as basal principles of organic evolution, the stronger must become our persuasion that discriminate breeding leads to divergence of type, while indiscriminate breeding leads to uniformity. This, in fact, is securely based on what we know from the experience supplied by artificial selection, which consists in the intentional mating of like with like to the [Pg 7] exclusion of unlike.

The point, then, which in the first instance must be firmly fastened in our minds is this:—so long as there is free intercrossing, heredity cancels variability, and makes in favour of fixity of type. Only when assisted by some form of discriminate isolation, which determines the exclusive breeding of like with like, can heredity make in favour of change of type, or lead to what we understand by organic evolution.

Now the forms of discriminate isolation, or homogamy, are very numerous. When, for example, any section of a species adopts somewhat different habits of life, or occupies a somewhat different station in the economy of nature, homogamy arises within that section. There are forms of homogamy on which Darwin has laid great stress, as we shall presently find. Again, when for these or any other reasons a section of a species becomes in any small degree modified as to form or colour, if the species happens to be one where any psychological preference in pairing can be exercised—as is very generally the case among the higher animals—exclusive breeding is apt to ensue as a result of such preference; for there is abundant evidence to show that, both in birds and mammals, sexual selection is usually opposed to the intercrossing of dissimilar varieties. Once more, in the case of plants, intercrossing of dissimilar varieties may be prevented by any slight difference in their seasons of flowering, of topographical stations, or even, in the case of flowers which depend on insects for their fertilization, by differences in the instincts and preferences of their visitors.

But, without at present going into detail with regard to these different forms of discriminate [Pg 8] isolation, there are still two others, both of which are of much greater importance than any that I have hitherto named. Indeed, these two forms are of such immeasurable importance, that were it not for their virtually ubiquitous operation, the process of organic evolution could never have begun, nor, having begun, continued.

The first of these two forms is sexual incompatibility—either partial or absolute—between different taxonomic groups. If all hares and rabbits, for example, were as fertile with one another as they are within their own respective species, there can be no doubt that sooner or later, and on common areas, the two types would fuse into one. And similarly, if the bar of sterility could be thrown down as between all the species of a genus, or all the genera of a family, *not otherwise prevented from intercrossing*, in time all such species, or all such genera, would become blended into a single type. As a matter of fact, complete fertility, both of first crosses and of their resulting hybrids, is rare, even as between species of the same genus; while as between genera of the same family complete fertility does not appear ever to occur; and, of course, the same applies to all the higher taxonomic divisions. On the other hand, some degree of infertility is not unusual as between different varieties of the same species; and, wherever this is the case, it must clearly aid the further differentiation of those varieties. It will be my endeavour to show that in this latter connexion sexual incompatibility must be held to have taken an immensely important [Pg 9] part in the differentiation of varieties into species. But meanwhile we have only to observe that *wherever* such incompatibility is concerned, it is to be regarded as an isolating agency of the very first importance. And as it is of a character purely physiological, I have assigned to it the name Physiological Isolation; while for the particular case where this general principle is concerned in the origination of specific types, I have reserved the name Physiological Selection.

The other most important form of discriminate isolation to which I have alluded is Natural Selection. To some evolutionists it has seemed paradoxical thus to regard natural selection as a form of isolation; but a little thought will suffice to show that such is really the most accurate way of regarding it. For, as Mr. Gulick says, "Natural selection is the exclusive breeding of those better adapted to the environment: ... it is a process in which the fittest are prevented from crossing with the less fitted, by the exclusion of the less fitted." Therefore it is, strictly and accurately, a mode of isolation, where the isolation has reference to adaptation, and is secured in the most effectual of possible ways—i.e. by the destruction of all individuals whose intercrossing would interfere with the isolation. Indeed, the very term "natural *selection*" shows that the

principle is tacitly understood to be one of isolation, because this name was assigned to the principle by Darwin for the express purpose of marking the analogy that obtains between it and the intentional isolation which is practised by breeders, fanciers, and horticulturists. The only difference between "natural selection" and "artificial selection" consists in this—that under the [Pg 10] former process the excluded individuals must necessarily perish, while under the latter they need not do so. But clearly this difference is accidental: it is in no way essential to the process considered as a process of discriminate isolation. For, as far as homogamous breeding is concerned, it can matter nothing whether the exclusion of the dissimilar individuals is effected by separation or by death.

Natural selection, then, is thus unquestionably a form of isolation of the discriminate kind; and therefore, notwithstanding its unique importance in certain respects, considered as a principle of organic evolution it is less fundamental—and also less extensive—than the principle of isolation in general. In other words, it is but a part of a much larger whole. It is but a particular form of a general principle, which, as just shown, presents many other forms, not only of the discriminate, but likewise of the indiscriminate kind. Or, reverting to the terminology of logic, it is a sub-species of the species Homogamy, which in its turn is but a constituent part of the genus Isolation.

So much then for homogamy, or isolation of the discriminate order. Passing on now to apogamy, or isolation of the indiscriminate kind, we may well be disposed, at first sight, to conclude that this kind of isolation can count for nothing in the process of evolution. For if the fundamental importance of isolation in the production of organic forms be due to its segregation of like with like, does it not follow that any form of isolation which is indiscriminate must fail to supply the very condition on which all the forms of discriminate isolation depend for their efficacy in the [Pg 11] causing of organic evolution? Or, to return to our concrete example, is it not self-evident that the farmer who separated his stock into two or more parts indiscriminately, would not effect any more change in his stock than if he had left them all to breed together?

Well, although at first sight this seems self-evident, it is in fact untrue. For, unless the individuals which are indiscriminately isolated happen to be a very large number, sooner or later their progeny will come to differ from that of the parent type, or unisolated portion of the previous stock. And, of course, as soon as this change of type begins, the isolation ceases to be indiscriminate: the previous apogamy has been converted into homogamy, with the usual result of causing a divergence of type. The reason why progeny of an indiscriminately isolated section of an originally uniform stock—e.g. of a species—will eventually deviate from the original type is, to quote Mr. Gulick, as follows:—"No two portions of a species possess exactly the same average character, and, therefore, the initial differences are for ever reacting on the environment and on each other in such a way as to ensure increasing divergence as long as the individuals of the two groups are kept from intergenerating[5]." Or, as I stated this principle in my essay on *Physiological Selection*, published but a short time before Mr. Gulick's invaluable contributions to these topics:—

> As a matter of fact, we find that no one individual "is like another all in all"; which is [Pg 12] another way of saying that a specific type may be regarded as the average mean of all its individual variations, any considerable departure from this average being, however, checked by intercrossing.... Consequently, if from any cause a section of a species is prevented from intercrossing with the rest of its species, we might expect that new varieties should arise within that section, and that in time these varieties should pass into new species. And this is just what we do find[6].

The name which I gave to this cause of specific change was Independent Variability, or variability in the absence of overwhelming intercrossing. But it now appears to me that this cause is really identical with that which was previously enunciated by Delbœuf. Again, in his important essay on *The Influence of Isolation*, Weismann concludes, on the basis of a large accumulation of facts, that the constancy of any given specific type "does not arise suddenly, but gradually, and is established by the promiscuous intercrossing of all individuals." From which, he says, it follows, that this constancy must cease so soon as the condition which maintains it ceases—i. e. so soon as intercrossing (Panmixia) between all individuals ceases, or so soon as a portion of a species is isolated from its parent stock. To this principle he assigns the name of Amixia. But Weismann's Amixia differs from my Independent Variability in several important particulars; and on this account I have designedly abstained from adopting his term. Here it is enough to remark that it [Pg 13] answers to the generic term Isolation, without reference to the *kind* of isolation as discriminate or indiscriminate, homogamous or apogamous. On the other hand, my Independent Variability is merely a re-statement of the so-called "Law of Delbœuf," which, in his own words, is as follows:—

> One point, however, is definitely attained. It is that the proposition, which further back we designated paradoxical, is rigorously true, A constant cause of variation, however insignificant it may be, changes the uniformity [of type] little by little, and diversifies it *ad infinitum*. From the homogeneous, left to itself, only the homogeneous can proceed; but if there be a slight disturbance ["léger ferment"] in the homogeneous, the homogeneity will be invaded at a single point, differentiation will penetrate the whole, and, after a time—it may be an infinite time—the differentiation will have disintegrated it altogether.

In other words, the "Law," which Delbœuf has formulated on mathematical grounds, and with

express reference to the question of segregate breeding, proves that, no matter how infinitesimally small the difference may be between the average qualities of an isolated section of a species compared with the average qualities of the rest of that species, if the isolation continues sufficiently long, differentiation of specific type is necessarily bound to ensue. But, to make this mathematical law biologically complete, it ought to be added that the time required for the change of type to supervene (supposing apogamy to be the only agent of change) will be governed by the range of individual variability which the species in question presents. A highly stable species (such as the Goose) might require an immensely long time for apogamy alone to [Pg 14] produce any change of type in an isolated portion of the species, while a highly variable species (such as the Ruff) would rapidly change in any portion that might be indiscriminately isolated. It was in order to recognize this additional and very important factor that I chose the name Independent *Variability* whereby to designate the diversifying influence of merely indiscriminate isolation, or apogamy. Later on Mr. Gulick published his elaborate papers upon the divergence of type under all kinds of isolation; and retained my term Independent, but changed Variability into Generation. I point this out merely for the sake of remarking that his Independent Generation is exactly the same principle as my Independent Variability, and Delbœuf's Mathematical Law.

Now, while I fully agree with Mons. Giard where he says, in the introductory lecture of his course on *The Factors of Evolution*[7], that sufficient attention has not been hitherto given by naturalists to this important factor of organic evolution (apogamy), I think I have shown that among those naturalists who have considered it there is a sufficient amount of agreement. *Per contra*, I have to note the opinion of Mr. Wallace, who steadily maintains the impossibility of any cause other than natural selection (i.e. one of the forms of homogamy) having been concerned in the evolution of species. But at present it is enough to remark that even Professor Ray Lankester—whose leanings of late years have been to the side of ultra-Darwinism, and who is therefore disposed to agree with Mr. Wallace wherever this is logically possible—even Professor Ray [Pg 15] Lankester observes:—

> Mr. Wallace does not, in my judgement, give sufficient grounds for rejecting the proposition which he indicates as the main point of Mr. Gulick's valuable essay on *Divergent Evolution through Cumulative Segregation*. Mr. Gulick's idea is that ... no two portions of a species possess exactly the same average character, and the initial differences will, if the individuals of the two groups are kept from intercrossing, assert themselves continuously by heredity in such a way as to ensure an increasing divergence of the forms belonging to the two groups, amounting to what is recognized as specific distinction. Mr. Gulick's idea is simply the recognition of a permanence or persistency in heredity, which, *caeteris paribus*, gives a twist or direction to the variations of the descendants of one individual as compared with the descendants of another[8].

Now we have seen that "Mr. Gulick's idea," although independently conceived by him, had been several times propounded before; and it is partly implicated in more than one passage of the *Origin of Species*, where free intercrossing, or the *absence* of isolation, is alluded to as maintaining the *constancy* of a specific type[9]. Moreover, it is still more fully recognized in the last edition of the *Variation of Animals and Plants*, where a paragraph is added for the purpose of sanctioning the principle in the imperfect form that it was stated by Weismann[10]. Nevertheless, to Mr. Gulick belongs the credit, not only of having been the first to conceive (though the last to publish) the "idea" in question, and of having stated it with greater fullness than anybody else; but still more of having verified its importance as a factor of organic evolution. [Pg 16]

For, in point of fact, Mr. Gulick was led to his recognition of the principle in question, not by any deductive reasoning from general principles, but by his own particular and detailed observations of the land mollusca of the Sandwich Islands. Here there are an immense number of varieties belonging to several genera; but every variety is restricted, not merely to the same island, but actually to the same valley. Moreover, on tracing this fauna from valley to valley, it is apparent that a slight variation in the occupants of valley 2 as compared with those of the adjacent valley 1, becomes more pronounced in the next—valley 3, still more so in 4, &c., &c. Thus it was possible, as Mr. Gulick says, roughly to estimate the amount of divergence between the occupants of any two given valleys by measuring the number of miles between them.

As already stated, I have myself examined his wonderful collection of shells, together with a topographical map of the district; and therefore I am in a position to testify to the great value of Mr. Gulick's work in this connexion, as in that of the utility question previously considered. The variations, which affect scores of species, and themselves eventually run into fully specific distinctions, are all more or less finely graduated as they pass from one isolated region to the next; and they have reference to changes of form and colour, which in no one case presents any appearance of utility. Therefore—and especially in view of the fact that, as far as he could ascertain, the environment in the different valleys was essentially the same—no one who [Pg 17] examines this collection can wonder that Mr. Gulick attributes the results which he has observed to the influence of apogamy alone, without any reference to utility or natural selection.

To this solid array of remarkable facts Mr. Wallace has nothing further to oppose than his customary appeal to the argument from ignorance, grounded on the usual assumption that no principle other than natural selection *can* be responsible for even the minutest changes of form or colour. For my own part, I must confess that I have never been so deeply impressed by the dominating influence of the *a priori* method as I was on reading Mr. Wallace's criticism of Mr.

Gulick's paper, after having seen the material on which this paper is founded. To argue that every one of some twenty contiguous valleys in the area of the same small island must necessarily present such differences of environment that all the shells in each are differently modified thereby, while in no one out of the hundreds of cases of modification in minute respects of form and colour can any human being suggest an adaptive reason therefor—to argue thus is merely to affirm an intrinsically improbable dogma in the presence of a great and consistent array of opposing facts.

I have laid special stress on this particular case of the Sandwich Islands' mollusca, because the fifteen years of labour which Mr. Gulick has devoted to their exhaustive working out have yielded results more complete and suggestive than any which so far have been forthcoming with regard to the effects of isolation in divergent evolution. But, if space permitted, it would be easy to [Pg 18] present abundance of additional facts from other sources, all bearing to the same conclusion—namely, that as a matter of direct observation, no less than of general reasoning, any unprejudiced mind will concede to the principle of indiscriminate isolation an important share in the origination of organic types. For as indiscriminate isolation is thus seen sooner or later to become discriminate, and as we have already seen that discriminate isolation is a necessary condition to all or any modification, we can only conclude that isolation in both its kinds takes rank with heredity and variability as one of the three basal principles of organic evolution.

Having got thus far in the way of generalities, we must next observe sundry further matters of comparative detail.

1. In any case of indiscriminate isolation, or apogamy, the larger the bulk of the isolated section the more nearly must its average qualities resemble those of its parent stock; and, therefore, the less divergence of character will ensue in a given time from this cause alone. For instance, if one-fourth of a large species were to be separated from the other three-fourths (say, by subsidence causing a discontinuity of area), it would continue the specific characters unchanged for an indefinitely long time, so far as the influence of such an indiscriminate isolation is concerned. But, on the other hand, if only half a dozen individuals were to be thus separated from the rest of their species, a comparatively short time would be needed for their descendants to undergo some varietal modification at the hands of apogamy. For, in this case, the chances would be infinitely [Pg 19] against the average characters of the original half-dozen individuals exactly coinciding with those of all the rest of their species.

2. In any case of homogamy, however, it is immaterial what proportional number of individuals are isolated in the first instance. For the isolation is here discriminate, or effected by the initial difference of the average qualities themselves—a difference, therefore, which presupposes divergence as having already commenced, and equally bound to proceed whether the number of intergenerants be large or small.

It may here be remarked that, in his essay on the *Influence of Isolation*, Professor Weismann fails to distinguish between the two kinds of isolation. This essay deals only with one of the many different forms of isolation—the geographical—and is therefore throughout concerned with a consideration of diversity as arising from apogamy alone. But in dealing with this side of the matter Weismann anticipated both Gulick and myself in pointing out the law of inverse proportion, which I have stated in the preceding paragraph in what appears to me its strictly accurate form.

3. Segregate Breeding, or homogamy, which arises under any of the many forms of discriminate isolation, must always tend to be *cumulative*. For, again to quote Mr. Gulick, who has constituted this fact the most prominent as it is the most original feature of his essay, "In the first place, every new form of Segregation[11] that now appears depends on, and is superimposed upon, [Pg 20] forms of Segregation that have been previously induced; for when Negative Segregation arises [i. e. isolation due to mutual sterility], and the varieties of a species become less and less fertile with one another, the complete infertility that has existed between them and some other species does not disappear, nor does the Positive Segregation cease [i. e. any other form of isolation previously existing].... In the second place, whenever Segregation is directly produced by some quality of the organism, variations that possess the endowment in a superior degree will have a larger share in producing the segregated forms of the next generation, and accordingly the segregative endowment of the next generation will be greater than that of the present generation; and so with each successive generation the segregation will become increasingly complete." And to this it may be added, in the third place, that where the segregation (isolation) is due to the external conditions of life under which the organism is placed, or where it is due to natural selection simultaneously operating in divergent lines of evolution, the same remarks apply. Hence it follows that discriminate isolation is, in all its forms, cumulative.

4. The next point to be noted is, that the cumulative divergence of type thus induced can take place only in as many different lines as there are different *cases* of isolation. This is a point which Mr. Gulick has not expressly noticed; but it is one that ought to be clearly recognized. Seeing that isolation secures the breeding of similar forms by exclusion (immediate or eventual) of those which are dissimilar, and that only in as far as it does this can it be a factor in organic evolution, [Pg 21] it follows that the resulting segregation, even though cumulative, can only lead to divergence of organic types in as many directions as there are cases of isolation. For any one group of

intergenerants only *serial* transformation is possible, even though the transformation be cumulative through successive generations in the single line of change. But there is always a probability that during the course of such *serial transformation in time*, some other case of isolation may supervene, so as to divide the previously isolated group of intergenerants into two or more further isolated groups. Then, of course, opportunity will be furnished for *divergent transformation in space*—and this in as many different lines as there are now different homogamous groups.

That this must be so is further evident, if we reflect that the evolutionary power of isolation depends, not only on the *preventing* of intercrossing between the isolated portion of a species and the rest of that species, but also upon the *permitting* of intercrossing between all individuals of the isolated portion, whereby the peculiar average of qualities which they as a whole present may be allowed to assert itself in their progeny—or, if the isolation has been from the first discriminate, whereby the resulting homogamy may thus be allowed to assert itself. Hence any one case of either species of isolation, discriminate or indiscriminate, can only give rise to what Mr. Gulick has aptly called "monotypic evolution," or a chain-like series of types arising successively in time, as distinguished from what he has called "polytypic evolution," or an [Pg 22] arborescent multiplication of types arising simultaneously in space.

For example, let us again take the geographical form of isolation. Where a single small intergenerant group of individuals is separated from the rest of its species—say, on an oceanic island—*monotypic* evolution may take place through a continuous and cumulative course of independent variation in a single line of change: all the *individuals* composing any one given generation will closely resemble one another, although the *type* may be progressively altering through a long series of generations. But if the original species had had two small colonies separated from itself (one on each of two different islands, so giving rise to two cases of isolation), then *polytypic* evolution would have ensued to the extent of there having been two different lines of evolution going on simultaneously (one upon each of the two islands concerned). Similarly, of course, if there had been three or four such colonies, there would have been three or four divergent lines of evolution, and so on.

5. In the *cases* of isolation just supposed there is only one *form* of isolation; and it is thus shown that under one form of isolation there may be as many lines of divergence as there are separate cases of such isolation. But now suppose that there are two or more forms of isolation—for instance, that on the same oceanic island the original colony has begun to segregate into secondary groups under the influence of natural selection, sexual selection, physiological selection, or any of the other forms of isolation—then there will be as many lines of divergent [Pg 23] evolution going on at the same time (and here on the same area) as there are forms of isolation affecting the oceanic colony. And this because each of the *forms* of isolation has given rise to a different *case* of isolation.

Now, inasmuch as different forms of isolation, when thus superadded one to another, constitute different cases of isolation, we may lay down the following general law as applying to all the forms of isolation—namely, *The number of possible directions in which divergent evolution can occur, is never greater than, though it may be equal to, the number of cases of efficient isolation —or the number of efficiently separated groups of intergenerants.*

6. We have now to consider with some care the particular and highly important form of isolation that is presented by natural selection. For while this form of isolation resembles all the other forms of the discriminate kind in that it secures homogamy, there are two points in which it differs from all of them, and one point in which it differs from most of them.

Natural selection differs from *all* the other known forms of isolation (whether discriminate or indiscriminate) in that it has exclusive reference to *adaptations* on the one hand, and, on the other hand, necessitates not only the elimination, but the destruction of the excluded individuals. Again, natural selection differs from *most* of the other forms of isolation in that, unless assisted by some other form, it can never lead to polytypic, but only to monotypic evolution. The first two points of difference are here immaterial; but the last is one of the highest importance, as we shall [Pg 24] immediately perceive.

In nearly all the other forms of isolation, polytypic or divergent evolution may arise under the influence of that form alone, or without the necessary co-operation of any other form. This we have already seen, for example, in regard to geographical isolation, under which there may be as many different lines of transmutation going on simultaneously as there are different cases of isolation—say, in so many different oceanic islands. Again, in regard to physiological isolation the same remark obviously applies; for it is evident that even upon the same geographical area there may be as many different lines of transmutation going on simultaneously as there are cases of this form of isolation. The bar of mutual sterility, whenever and wherever it occurs, must always render polytypic evolution possible. And so it is with almost all the other forms of isolation: that is to say, one *form* does not necessarily require the assistance of another *form* in order to create an additional *case* of isolation. But it is a peculiarity of natural selection, considered as a form of isolation, that it does necessarily require the assistance of some other form before it can give rise to an additional case of isolation; and therefore before it can give rise to any *divergence* of character in ramifying lines, as distinguished from *transformation* of characters in a single line. Or, in other words, natural selection, when acting alone, can never induce polytypic evolution, but only monotypic.

That this important conclusion is a necessary deduction from the theory of natural selection

itself, a very few words will be enough to show. For, according to the theory, survival of the fittest is a form of isolation which acts through utility, by *destroying* all the individuals whom it fails to isolate. Hence it follows that survival of the fittest is a form of isolation which, if acting alone, cannot *possibly* effect divergent evolution. For, in the first place, there is nothing in this form of isolation to ensure that the fitter individuals should fail to interbreed with the less fit which are able to survive; and, in the second place, in all cases where the less fit are not sufficiently fit to be suffered to breed, they are exterminated—i. e. not permitted to form a distinct variety of their own. If it be said that survival of the fittest may develop simultaneously two or more lines of *useful* change, the answer is that it can only do this if each of the developing varieties is isolated from the others by some *additional form* of isolation; for, if not, there can be no commencement of utilitarian *divergence*, since whatever number of utilitarian changes may be in course of simultaneous development, they must in this case be all blended together in a single line of specific transmutation. Nay, even if specific divergence has actually been commenced by natural selection when associated with some other form of homogamy, if the latter should afterwards be withdrawn, natural selection would then be unable to maintain even so much divergence of character as may already have been attained: free intercrossing between the two collateral, and no longer isolated branches, would ensure their eventual blending into a common stock. Therefore, I repeat, natural selection, when acting alone, can never induce polytypic evolution, but only monotypic. [Pg 25] [Pg 26]

Now I regret to say that here, for the first and only time throughout the whole course of the present treatise, I find myself in seeming opposition to the views of Darwin. For it was the decidedly expressed opinion of Darwin that natural selection *is* competent to effect polytypic, or divergent, evolution. Nevertheless, I believe that the opposition is to a large extent only apparent, or due merely to the fact that Darwin did not explicitly state certain considerations which throughout his discussion on "divergence of character" are seemingly implied. But, be this as it may, I have not even appeared to desert his leadership on a matter of such high importance without having duly considered the question in all its bearings, and to the utmost limit of my ability. Moreover, about two years after the publication of my first paper[12] upon the subject, Mr. Gulick followed, at somewhat greater length, in the same line of dissent. Like all the rest of his work, this is so severely logical in statement, as well as profoundly thought out in substance, that I do not see how it is possible for any one to read impartially what he has written, and then continue to hold that natural selection, if unassisted by any other form of isolation, can possibly effect divergence of character—or polytypic as distinguished from monotypic evolution[13].

I may here quote from Mr. Gulick's paper three propositions, serving to state three large and general bodies of observable fact, which severally and collectively go to verify, with an overwhelming mass of evidence, the conclusion previously reached on grounds of general reasoning. [Pg 27]

> The facts of geographical distribution seem to me to justify the following statements:—
>
> (1) A species exposed to different conditions in the different parts of the area over which it is distributed, is not represented by divergent forms when free interbreeding exists between the inhabitants of the different districts. In other words, Diversity of Natural Selection without Separation does not produce divergent evolution.
>
> (2) We find many cases in which areas, corresponding in the character of the environment, but separated from each other by important barriers, are the homes of divergent forms of the same or allied species.
>
> (3) In cases where the separation has been long continued, and the external conditions are the most diverse in points that involve diversity of adaptation, there we find the most decided divergences in the organic forms. That is, where Separation and Divergent Selection have long acted, the results are found to be the greatest.
>
> The 1st and 3rd of these propositions will probably be disputed by few, if by any. The proof of the 2nd is found wherever a set of closely allied organisms is so distributed over a territory that each species and variety occupies its own narrow district, within which it is shut by barriers that restrain its distribution while each species of the environing types is distributed over the whole territory. The distribution of terrestrial molluscs on the Sandwich Islands presents a great body of facts of this kind.

CHAPTER II. [Pg 28]
ISOLATION (*continued*).

I will now recapitulate the main doctrines which have been set forth in the foregoing chapter, and then proceed to consider the objections which have been advanced against them.

It must be remembered that by isolation I mean exactly what Mr. Gulick does by "Segregation," and approximately what Professor Weismann does by "Amixia "—i. e. the prevention of intercrossing.

Isolation occurs in very many forms besides the geographical, as will be more fully shown at the

end of this chapter; and in all its forms it admits of degrees.

It also occurs in two very different species or kinds—namely, discriminate and indiscriminate. These I have called respectively Homogamy and Apogamy. This all-important distinction has been clearly recognized by Mr. Gulick, as a result of his own thought and observation, independently of anything that I have published upon the subject.

In view of this distinction Isolation takes rank with Heredity and Variability as one of the most fundamental principles of organic evolution. For, if these other two principles be granted, the [Pg 29] whole theory of descent resolves itself into an inquiry touching the causes, forms, and degrees of Homogamy.

Save in cases where very large populations are concerned, apogamy must sooner or later give rise *per se* to homogamy, owing to the Law of Delbœuf. which is the principle that I have called Independent Variability, and Gulick has called Independent Generation. But of course this does not hinder that under apogamy various other causes of homogamy are likely to arise—in particular natural selection.

That natural selection differs from most of the other forms of isolation in not being capable of causing *divergent* or *polytypic* evolution must at once become evident, if we remember that the only way in which isolation of any form can cause such evolution is by partitioning a given group of intergenerants into two or more groups, each of which is able to survive as thus separated from the other, and so to carry on the evolution in divergent lines. But the distinguishing peculiarity of natural selection, considered as a form of isolation, is that it effects the isolation *by killing off all the individuals which it fails to isolate*: consequently, this form of isolation differs from other forms in prohibiting the possibility of any ramification of a single group of intergenerants into two or more groups, for the purpose of carrying on the evolution in divergent lines. Therefore, under this form of isolation alone, evolution must proceed, palm-like, in a single line of growth. So to speak, the successive generations continuously ascend to higher things on the steps supplied by their own "dead selves"; but in doing so they must climb a single ladder, no [Pg 30] rung of which can be allowed to bifurcate in the presence of the uniformity secured *for that generation* by the free intercrossing of the most fit. Even though beneficial variations may arise in two or more directions simultaneously, and all be simultaneously selected by survival of the fittest, the effect of free intercrossing (in the absence of any other form of isolation) will be to fuse all these beneficial variations into one common type, and so to end in *monotypic* evolution as before. In order to secure *polytypic* evolution, intercrossing between the different beneficial variants which may arise must be prevented; and there is nothing to prevent such intercrossing in the process of natural selection *per se*. In order that the original group of intergenerants should be divided and sub-divided into two or more groups of intergenerants, some additional form of isolation must necessarily supervene—when, of course, polytypic evolution will result. And, as Mr. Gulick has shown, the conclusion thus established by deductive reasoning is verified inductively by the facts of geographical distribution.

How, then, are we to account for the fact that Darwin attributed to natural selection the power to cause divergence of character? The answer is sufficiently simple. *He does so by tacitly invoking the aid of some other form of homogamy in every case.* If we carefully read pp. 86-97 of the *Origin of Species*, where this subject is under consideration, we shall find that in every one of the arguments and illustrations which are adduced to prove the power of natural selection to effect "divergence of character," he either pre-supposes or actually names some other form of homogamy as the originating cause of the diversity that is afterwards presented to natural [Pg 31] selection for further intensification. To give only one example. At the starting-point of the whole discussion the priority of such other forms of homogamy is assumed in the following words:—

> But how, it may be asked, can any analogous principle [to that of diversity caused by artificial selection] apply in nature? I believe it can and does apply most efficiently (though it was a long time before I saw how), 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 polity of nature, and so be enabled to increase in numbers.

Now, without question, so soon as segregate breeding in two or more lines of homogamy has been in any sufficient degree determined by some "change of structure, constitution, or habits," natural selection will forthwith proceed to increase the divergence in as many different lines as there are thus yielded discriminately isolated sections of the species. And this fact it must have been that Darwin really had before his mind when he argued that diversification of character is caused by natural selection, through the benefit gained by the diversified forms being thus "enabled to increase in number." Nevertheless he does not expressly state the essential point, that although diversification of character, *when once begun*, is thus *promoted* by natural selection, which forthwith proceeds to cultivate each of the resulting branches, yet diversification of character can never be *originated* by natural selection. The change of "structure," of "constitution," of "habits," of "station," of geographical area, of reciprocal fertility, and so on— [Pg 32] this change, *whatever* it may have been, must clearly have been antecedent to any operation of natural selection through the benefit which arose from the change. Therefore the change must in all cases have been due, in the first instance, to some other form of isolation than the superadded form which afterwards arose from superior fitness in the possession of superior benefit—although, so long as the prior form of isolation endured, or continued to furnish the necessary

condition to the co-operation of survival of the fittest, survival of the fittest would have continued to increase the divergence of character in as many ramifying lines as there were thus given to its action separate cases of isolation by other means.

In short, as divergence of character must in all cases be due to a prevention of intercrossing, and as in the process of natural selection there is, *ex hypothesi*, nothing to prevent the intercrossing until the divergence has already arisen, to suppose that natural selection alone can have caused the divergence, is to suppose that natural selection can have caused the conditions of its own activity, which is absurd.

Seeing, then, that even in cases where any "benefit" arises from divergence of character, such benefit can arise only after the divergence has already commenced, and seeing that on this as on other accounts previously mentioned it is plainly impossible to attribute the origin of such divergence to natural selection, we find that natural selection must be in all cases assisted by some other form of isolation, if it is to be concerned in polytypic as distinguished from monotypic evolution. But this does not hinder that, when it is so assisted, natural selection may become— [Pg 33] and, I believe, does become—the most efficient of all the forms of isolation in promoting divergence of character. For, in the first place, of all the forms of isolation natural selection is probably the most energetic in promoting monotypic evolution; so that under the influence of such isolation monotypic evolution probably advances more rapidly than it does under any other form of isolation. In the second place, when polytypic evolution has been begun by any of these other forms of isolation, and natural selection then sets to work on each of the resulting branches, although natural selection is thus engaged in as many different acts of monotypic evolution as there are thus separate cases supplied to it by these other forms of isolation, the joint result of all these different acts is to hurry on the polytypic evolution which was originally started by the other forms of isolation. So to speak, natural selection is the forcing heat, acting simultaneously on each of the separate branches which has been induced to sprout by other means; and in thus rapidly advancing the growth of all the branches, it is still entitled to be regarded as the most important *single* cause of diversification in organic nature, although we must henceforth cease to regard it as in any instance the *originating* cause—or even so much as the *sustaining* cause.

So much by way of summary and recapitulation. I will now briefly consider the only objections which, so far as I can see, admit of being brought against the foregoing doctrine of Isolation as held by Mr. Gulick and myself. These possible objections are but two in number—although but [Pg 34] one of them has been hitherto adduced. This, therefore, I will take first.

Mr. Wallace, with his customary desire to show that natural selection is everywhere of itself capable of causing organic evolution, seeks to minimize the swamping effects of free intercrossing, and the consequent importance of other forms of isolation. His argument is as follows.

Alluding to the researches of Mr. J. A. Allen, and others, on the amount of variation presented by individuals of a species in a state of nature, Mr. Wallace shows that, as regards any given part of the animal under consideration, there is always to be found a considerable range of individual variation round the average mean which goes to constitute the specific character of the type. Thus, for example, Mr. Allen says of American birds, "that a variation of from fifteen to twenty per cent. in general size, and an equal degree of variation in the relative size of different parts, may be ordinarily expected among specimens from the same species and sex, taken at the same locality, while in some cases the variation is even greater than this." Now, Mr. Wallace is under the impression that these facts obviate the difficulty which arises from the presence of free intercrossing—the difficulty, that is, against the theory of natural selection when natural selection is supposed to have been the exclusive means of modification. For, as he says, "if less size of body would be beneficial, then, as half the variations in size are above and half below the mean or existing standard of the species, there would be ample beneficial variations"; and [Pg 35] similarly with regard to longer or shorter legs, wings, tails, &c., darker or lighter colour, and so on through all the parts of any given organism.

Well, although I have no wish at all to disparage the biological value of these actual measurements of the range of individual variation, I must point out that they are without any value at all in the connexion which Mr. Wallace adduces them. We did not require these measurements to tell us the broad and patent fact that "no being on this earthly ball is like another all in all"—or, in less Tennysonian words, that as regards every specific structure there is a certain amount of individual variability round an average mean. Indeed, in my own paper on *Physiological Selection*—against which Mr. Wallace is here specially arguing—I expressly said, as previously remarked, "that a specific type may be regarded as *the average mean of all individual variations*." The fact of such individual variability round a specific mean has always been well known to anatomists; it constitutes one of the basal pillars of the whole Darwinian theory; and is besides a matter of universal recognition as regards human stature, features, and so forth. The value of Mr. Allen's work consists in accurately measuring the *amount* or *range* of individual variation; but the question of its amount or range is without relevancy in the present connexion. For the desirability of isolation as an aid to natural selection even where monotypic evolution is concerned, does not arise with any reference to the amount or range of variation: it arises with reference to the *number* of variations which are—or are not—*similar* and *simultaneous*. If there [Pg 36] be a sufficient number which are both similar and simultaneous, the desirability of any co-operating form of isolation is correspondingly removed, because natural selection may then have sufficient material wherewith to overcome the adverse influence of free intercrossing, and so of

itself to produce monotypic evolution. Now, variations may be numerous, similar, and simultaneous, either on account of some common cause acting on many individuals at the same time, or on account of the structures in question being more or less variable round a specific mean. In the latter case—which is the only case that Mr. Allen's measurements have to do with—the law of averages will of course determine that half the whole number of variations in any given structure, in any given generation, will be above the mean line. But, equally of course, no one has ever denied that where, for either of these reasons, natural selection is provided with sufficient material, it is correspondingly capable of improving the specific type without the assistance of any other form of homogamy; so to speak, they protect themselves by their very numbers, and their superiority over others leads to their survival and accumulation. But what is the result? *The result can only be monotypic evolution.* No matter how great the number, or how great the range, of variations round an average specific mean, out of such material natural selection can never produce *polytypic* evolution: it may *change* the type to any extent during successive generations, and in a single line of change; but it cannot *branch* the type, unless some other form of homogamy intervenes. Therefore, when Mr. Wallace adduces the well-known fact that all [Pg 37] structures vary more or less round a specific mean as proof that natural selection need not be incommoded by free intercrossing, but can of itself produce all the known phenomena of specific evolution, he fails to perceive that his argument refers only to one aspect of such evolution (viz. the transformation of species in time), and does not apply to the aspect with which alone my paper on *Physiological Selection* was concerned (viz. the multiplication of species in space).

The same thing may be shown in this way. It is perfectly obvious that where the improvement of type in a linear series is concerned (monotypic evolution), free intercrossing, far from being a hindrance to the process, *is the very means by which the process is accomplished*. Improvement here ascends by successive steps, in successive generations, simply *because* of the general intercrossing of the generally most fit with the result that the species, *as a whole*, gradually becomes transformed into another species, *as a whole*. Therefore, it would be mere fatuity in any one to adduce free intercrossing as a "difficulty" against natural selection alone being competent to produce evolution of this kind. But where the kind of evolution is that whereby the species is *differentiated*—where it is required, for instance, to produce different structures in different portions of the species, such as the commencement of a fighting spur on the wing of a duck, or *novel* characters of any sort in different groups of the species—free intercrossing is no longer a condition to, but an absolute preventive of, the process; and, therefore, unless checked as between each portion of the species by some form of homogamy other than natural selection, it [Pg 38] must effectually inhibit any *segregation* of specific types, or divergence of character.

Hence it is that, while no Darwinian has ever questioned the power of unaided selection to cause *improvement of character in successive generations*, in common now with not a few other Darwinians I have emphatically denied so much as the abstract possibility of selection alone causing a *divergence of character in two or more simultaneous lines of change*.

And, although these opposite views cannot be reconciled, I am under the impression that they do admit of being explained. For I take them to indicate a continued failure to perceive the all-important distinction between evolution as monotypic and polytypic. Unless one has fully grasped this distinction, and constantly holds it in mind, he is not in a position to understand the "difficulty" in question; nor can he avoid playing fast and loose with natural selection as possibly the sole cause of evolution, and as necessarily requiring the co-operation of some other cause. But if he once clearly perceives that "evolution" is a logical genus, of which the monotypic and the polytypic forms are species, he will immediately escape from his confusion, and find that while the monotypic form may be caused by natural selection alone the polytypic form can never be so caused.

The second difficulty which I have to mention as at first sight attaching to the views of Mr. Gulick and myself on the subject of Isolation is, that in an isolated section of a species Mr. Francis Galton's law of regression in the average character of offspring to the typical character of the [Pg 39] group through reversion or atavism (*Natural Inheritance*, p. 97) must have the effect of neutralizing the segregative influence of mere apogamy. That such, however, cannot be the case has been well shown by Mr. Gulick in his paper on *Intensive Segregation*. Without at all disputing the validity of Mr. Galton's law, he proves that "it can hold in full force only where there is free crossing, otherwise no divergent race could ever be formed by any amount of selection and independent breeding[14]." This is so self-evident that I need not quote his demonstration of the point.

In conclusion, then, and having regard to the principle of isolation as a whole, or in all the many and varied forms in which this principle obtains, I trust that I have redeemed the promise with which I set out—viz. to show that in relation to the theory of descent this principle is of an importance second to no other, not even excepting heredity, variability, and the struggle for existence. This has now been fully shown, inasmuch as we have clearly seen that the importance of the struggle for existence, and consequent survival of the fittest, arises just because survival of the fittest is a form, and a very stringent form, of isolation; while, as regards both heredity and variability, we are now in a position to see that the more fully we recognize their supreme

importance as principles concerned in organic evolution, the more must we also recognize that any rational theory of such evolution becomes, in the last resort, a theory of the different modes [Pg 40] in which efficient isolation can be secured. For, in whatever degree the process of organic evolution has been dependent upon heredity with variability, in that degree must it also have been dependent upon the means of securing homogamy, whereby alone the force of heredity can be made to expend itself in the innumerable directions of progressive change, instead of continually neutralizing the force of variability by promiscuous intercrossing.

CHAPTER III. [Pg 41]

Physiological Selection.

So far we have been concerned with the principle of Isolation in general. We have now to consider that form of isolation which arises in consequence of mutual infertility between the members of any group of organisms and those of all other similarly isolated groups occupying simultaneously the same area.

Against the view that natural selection is a sufficient explanation of the origin of species, there are two fatal difficulties: one, the contrast between natural species and domesticated varieties in respect of cross-sterility; the other, the fact that natural selection cannot possibly give rise to polytypic as distinguished from monotypic evolution. Now it is my belief that the theory of physiological selection fully meets both these difficulties. Indeed I hold this to be undeniable in a formal or logical sense: the only question is as to the evidence which can be adduced for the theory in a practical or biological sense. Therefore in this chapter, where the theory has first of all to be stated, I shall restrict the exposition as much as possible to the former, leaving for subsequent consideration the biological side.

The following is a brief outline sketch of this theory[15]. [Pg 42]

Of all parts of those variable objects which we call organisms, the most variable is the reproductive system; and the variations may carry with them functional changes, which may be either in the direction of increased or of diminished fertility. Consequently variations in the way of greater or less fertility frequently take place, both in plants and animals; and probably, if we had adequate means of observing this point, we should find that there is no one variation more common. But of course where infertility 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 and to hand on the variation. If, however, the variant, while showing some degree of infertility with the parent form, continues to be as fertile as before when mated with similar variants, under these circumstances there is no reason why such differential fertility should not be perpetuated.

Stated in another form this suggestion enables us to regard many, if not most, species as the records of variations in the reproductive systems of their ancestors. When 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 arise in the reproductive system in the way here suggested, they tend to be preserved as new natural varieties, or incipient species. At first the difference would only be in respect of the reproductive systems; but eventually, on [Pg 43] account of independent variation, other differences would supervene, and the variety would take rank as a true species.

Now we must remember that physiological isolation is not like those other forms of isolation (e.g. geographical) which depend for their occurrence on accidents of the environment, and which may therefore take place suddenly in a full degree of completeness throughout a large section of a species. Physiological isolation depends upon distinctive characters belonging to organisms themselves; and it would be opposed to the whole theory of descent with progressive modification to imagine that absolute sterility usually arises, in a single generation between two sections of a perfectly fertile species. Therefore evolutionists must believe that in most, if not in all cases—could we trace the history, say of any two species, which having sprung from a single parent stock on a common area, are now absolutely sterile with one another—we should find that this mutual sterility had been itself a product of gradual evolution. Starting from complete fertility within the limits of a single parent species, the infertility between derivative or divergent species, *at whatever stage in their evolution this began to occur*, must usually at first have been well-nigh imperceptible, and thenceforth have proceeded to increase stage by stage.

But, if it be true that physiological isolation between genetically allied groups must usually itself have been the product of a gradual evolution; and if, when fully evolved, it constitutes a condition of the first importance to any further differentiation of these groups (by preventing fusion again [Pg 44] into one group, more or less resembling the original parent form), do we not perceive at least a strong probability that in the lower stages of its evolution such mutual infertility must have acted as a segregating influence between the diverging types, in a degree proportional to its own development? The importance of mutual sterility as a condition to divergent evolution is not

denied, *when this sterility is already present in an absolute degree*; and we have just seen that, before it can have attained to this absolute degree *it must presumably, and as a rule, itself have been the subject of a gradual development*. Does it not therefore become, on merely antecedent grounds, in a high degree probable, that from the moment of its inception this isolating agency must have played the part of a segregating cause, in a degree proportional to that of its completeness as a physiological character?

Whoever answers this question in the affirmative will have gone most of the way towards accepting, on merely antecedent grounds, the theory of physiological selection. And therefore it is that I have begun this statement of the theory by introducing it upon these grounds, thereby hoping to show how extremely simple—how almost self-evident—is the theory which it will now be my endeavour to substantiate. I may here add that the theory was foreshadowed by Mr. Belt in 1874[16], clearly enunciated in its main features by Mr. Catchpool in 1884[17], and very fully thought out by Mr. Gulick during a period of about fifteen years, although he did not publish until [Pg 45] a year after the appearance of my own paper in 1886[18].

I must next proceed to state some of the leading features of physiological selection in further detail.

It has already been shown that Darwin clearly perceived that the very general occurrence of some degree of infertility between allied species cannot possibly be attributed to the *direct* agency of natural selection. His explanation was that the slight structural modifications entailed by the transformation of one specific type into another, so react upon the highly delicate reproductive system of the changing type as to render it in some degree infertile with its parent type. Now the theory of physiological selection begins by traversing this view. It does not, however, deny that in *some* cases the morphological may be the prior change; but it strenuously denies that this must be so in *all* cases. Indeed, according to my statement in 1886, the theory inclines to the view that, *as a rule*, the physiological change is prior. At the same time, the theory, as I have always stated it, maintains that it is immaterial whether, "in the majority of instances," the physiological change has been prior to the morphological, or vice versa; since in either case the physiological change will equally make for divergence of character.

To show this clearly the best way will be to consider the two cases separately, taking first that in [Pg 46] which the physiological change has priority. In this case our theory regards any morphological changes which afterwards supervene as due to the independent variability which will sooner or later arise under the physiological isolation thus secured. But to whatever causes the subsequent morphological changes may be due, the point to notice is that they are as a general rule, consequent upon the physiological change. For in whatever *degree* such infertility arises between two sections of a species occupying the same area, in that *degree* is their interbreeding prevented, and, therefore, opportunity is given for a subsequent divergence of type, whether by the influence of independent variability alone, or also by that of natural selection, as now acting more or less independently on each of the partially separated groups. In short, all that was said in the foregoing chapters with respect to isolation in general, here applies to physiological isolation in particular; and by supposing such isolation to have been the prior change, we can as well understand the subsequent appearance of morphological divergence on continuous areas, as in other forms of isolation we can understand such divergence on discontinuous areas, seeing that even a moderate degree of cross-infertility may be as effectual for purposes of isolation as a high mountain-chain, or a thousand miles of ocean.

Here, then, are two sharply-defined theories to explain the very general fact of there being some greater or less degree of cross-infertility between allied species. The older, and hitherto current theory, supposes the cross-infertility to be but an *accident* of specific divergence, which, [Pg 47] therefore, has nothing to do with *causing* the divergence. The newer theory, on the other hand, supposes the cross-infertility to have often been a necessary *condition* to the divergence having begun at all. Let us now consider which theory has most evidence in its favour.

First of all we have to notice the very general occurrence of the fact in question. For when we include the infertility of hybrids, as well as first crosses, the occurrence of some degree of infertility between allied species is so usual that Mr. Wallace recommends experiments to ascertain whether careful observation might not prove, even of species which hybridize, "that such species, when crossed with their near allies, do always produce offspring which are more or less sterile *inter se*[19]." This seems going too far, but nevertheless it is the testimony of a highly competent naturalist to the very general occurrence of an association between the morphological differentiation of species and the fact of a physiological isolation. Now I regard it as little short of self-evident that this general association between mutual infertility and innumerable secondary, or relatively variable morphological distinctions, is due to the former having been an original and a necessary condition to the occurrence of the latter, in cases where intercrossing has not been otherwise prevented.

The importance of physiological isolation, *when once fully developed*, cannot be denied, for it is evident that if such isolation could be suddenly destroyed between two allied species occupying a common area, they would sooner or later become fused into a common type—supposing, of [Pg 48] course, no other form of isolation to be present. The necessity then for this physiological form of isolation in *maintaining* a specific differentiation which has been already *attained* cannot be disputed. Yet it has been regarded as "Darwinian heresy" to suggest that it can have been of any important service *during the process of attainment*, or while the specific differentiation is being advanced, and this notwithstanding that the physiological change must presumably have

developed *pari passu* with the morphological, and notwithstanding that in countless cases the former is associated with every conceivable variety of the latter.

Again, why should the physiological change be thus associated with *every conceivable variety* of morphological change? Throughout the length and breadth of both vegetable and animal kingdoms we find this association, in the great majority of cases, where new species arise. Therefore, on the supposition that in all such cases the physiological change has been adventitiously induced by the morphological changes, we have to face an apparently unanswerable question—Why should the reproductive mechanism of all organic beings have been thus arranged, as it were, to change in immediate response to the very slightest alteration in the complex harmony of "somatic" processes, which now more than ever is recognized as exercising so comparatively little influence on the *hereditary* endowments of this mechanism? Consider the difference between a worm and the bird that is eating it, an oak tree and the gall-insect that is piercing it: are we to suppose that in all cases, no matter how greatly the types differ, they must [Pg 49] agree in this, that when any parts of these complex structures change, ever so slightly, the reproductive system is almost certain to be adventitiously affected, yet always thus affected in the same peculiar way?

If it be answered that the reproductive system is known to be very sensitive to slight changes in the external conditions of life, the answer proves too much. For though this is true, yet our opponents must acknowledge that the reproductive system is not so sensitive, *in this particular respect*, as their interpretation of the origin of specific infertility requires. The proof of this point is overwhelming, for there is the evidence from the entire range of our domesticated productions, both vegetable and animal. Here the amount of structural change, which has been slowly accumulated by artificial selection, is often much greater in amount, and incomparably more rapid, than that which has been induced between allied species by natural selection; and yet there is scarcely any indication of the reproductive system having been affected in the particular way that our opponents' theory requires. There are many instances of its having been affected in sundry other ways (chiefly, however, without any accompanying morphological change); but among all the thousands of our more or less enormously modified artificial types, there is scarcely one instance of such a peculiar sexual relation between the modified descendants of a common type as so usually obtains between allied species in nature. Yet in all other respects evolutionists are bound to believe that the process of modification has been in both cases strictly [Pg 50] analogous. Why then this conspicuous difference with respect to the reproductive system?

The answer is simple. It has never been the object of breeders or of horticulturists to select variations in the direction of cross-infertility, for the swamping effects of intercrossing are much more easily and rapidly prevented by artificial isolation. Consequently, although they have been able to modify natural types in so many directions and in such high degrees with regard to *morphology*, there has been no accompanying physiological modification of the kind required. But in nature there is no such thing as artificial, i.e. intentional, isolation. Consequently, on common areas it must usually happen that those changes of morphology which are associated with cross-infertility are the only ones which can arise. Hence the very remarkable contrast between our domesticated varieties and natural species with regard to cross-infertility is just what the present theory would expect, or, indeed, require. But on any other theory it has hitherto remained inexplicable.

In particular, the contrast in question has constituted one of the main difficulties with which the theory of natural selection has hitherto had to contend, not only in the popular mind, but also in the judgement of naturalists, including the joint-authors of the theory themselves. Thus Darwin says:—

> The fertility of varieties is, with reference to my theory, of equal importance with the sterility of species, for it seems to make a broad and clear distinction between varieties and species[20].

And Mr. Wallace says:— [Pg 51]

> One of the greatest, or perhaps we may say the greatest, of all the difficulties in the way of accepting the theory of natural selection as a complete explanation of the origin of species, has been the remarkable difference between varieties and species in respect of fertility when crossed[21].

Now, in view of this conspicuous contrast, Darwin suggested that species in a state of nature "will have been exposed during long periods of time to more uniform conditions than have domesticated varieties, and [that] this may well make a wide difference in the result." Now we have to remember that species, living and extinct, are numbered by millions, and represent every variety of type, constitution, and habits; is it probable, then, that this one peculiarity of the reproductive system should be due, in so many cases, to some merely incidental effect produced on that system by uniform conditions of life? Again, *ex hypothesi*, at the time when a variety is first forming, the influence exercised by uniform conditions of life (whatever in different cases this may happen to be) cannot be present as regards that variety: yet this is just the time when its infertility with the parent (or allied) form is most likely to have arisen; for it is just then that the nascent variety would otherwise have been most liable to extinction by free intercrossing—even supposing that in the presence of such intercrossing the variety could ever have come into existence at all.

Mr. Wallace meets the difficulty by arguing that sterility between allied species may have been brought about by the direct influence of natural selection. But, as previously remarked, this view is expressly opposed to that of Darwin, who held that Wallace's contention is erroneous. [Pg 52]

It will be seen, then, that both Darwin, and Wallace, fully recognize the necessity of finding some explanation of the infertility of allied species, over and above the mere reaction of morphological differentiation on the physiology of the reproductive system, and they both agree in suggesting additional causes, though they entirely disagree as to what these causes are. Now, the theory of physiological selection likewise suggests an additional cause—or, rather, a new explanation—and one which is surely the most probable. For what is to be explained? The very general association of a certain physiological peculiarity with that amount of morphological change which distinguishes species from species, of whatever kind the change may be, and in whatever family of the animal or vegetable kingdom it may occur. Well, the theory of physiological selection explains this very general association by the simple supposition that, at least in a large number of cases, it was the physiological peculiarity which first of all led to the morphological divergence, by interposing the bar of sterility between two sections of a previously uniform species; and by thus isolating the two sections one from another, started each upon a subsequently independent course of divergent evolution.

Or, to put it in another way, if the occurrence of this physiological peculiarity has been often the only possible means of isolating two sections of a species occupying a common area, and thus giving rise to a divergence of specific type (as obviously *must* have been the case wherever there was an absence of any other form of isolation), it is nothing less than a necessary consequence that many allied species should now present the physiological peculiarity in question. Thus the association between the physiological peculiarity and the morphological divergence is explained by the simple hypothesis, that the former has acted as a necessary condition to the occurrence of the latter. In the absence of other forms of isolation, the morphological divergence could not have taken place at all, had not the physiological peculiarity arisen; and hence it is that we now meet with so many cases where such divergence is associated with this peculiarity. [Pg 53]

So far we have been considering the physiological change as historically the prior one. Here, at first sight, it may seem that the segregative power of physiological selection must end; for it may well seem impossible that the physiological change can ever be necessary for the divergence of morphological varieties into true species in cases where it has *not* been the prior change, but has only set in after morphological changes have proceeded far enough to have already constituted definite varieties. A little thought, however, will show that physiological selection is quite as potent a condition to the differentiation of species when it occurs after varietal divergence has begun, as it is when it occurs before the divergence—and hence that it really makes no difference to the theory of physiological selection whether, in particular cases, the cross-infertility arises before or after any structural or other modifications with which it is associated.

For the theory does not assert that all varieties have been due to physiological selection. There are doubtless many other causes of the origin of varieties besides cross-infertility with parent forms; but, as a general rule, it does not appear that they are by themselves capable of carrying divergence beyond a merely varietal stage. In order to carry divergence to the stage of producing *species*, it appears to be a general condition that, sooner or later, cross-infertility should arise—seeing that, when varieties do succeed in becoming species, we almost invariably find that, as a matter of fact, cross-infertility has arisen. Hence, if cross-infertility has thus usually been a necessary condition to a varietal divergence becoming specific, it can make no material difference when the incipient infertility arose. [Pg 54]

It may be asked, however, whether I suppose that, when the physiological change is subsequent, it is directly *caused* by change of structure, size, colour, &c., or that it arises, so to speak, accidentally, from other causes which may have affected the sexual system in the required way. To this question I may briefly reply, that, looking to the absence of any influence exercised on the reproductive systems of our domesticated plants and animals by the great and varied changes which so many of these forms present, it would seem that among natural varieties such closely analogous changes are presumably not the usual causes of the physiological change, even where the latter are subsequent to the former. Nevertheless, I do not deny that in some of these cases changes of structure, size, colour, &c., may be the causes of the physiological change by reacting on the sexual system in the required way. But in such cases free intercrossing will have prevented the perpetuation of any morphological changes, save those which have the power of so reacting on the reproductive system as to produce the physiological change, and thus to protect themselves against the full and adverse power of free intercrossing. We know that slight or initial changes of structure, colour, &c., frequently occur as varieties, and yet that on common areas very few of these varieties become distinct species: free intercrossing prevents any such further divergence of character. But if in the course of many such abortive attempts, as it were, to produce a new species, nature happens to hit upon a structural or a colour variation which is capable of reacting on the sexual system in the particular way required, then this variation will be enabled to protect itself against free intercrossing in proportion to its own development. Or, in other words, the more it develops as a morphological change, the more will it increase the physiological change; while the more the physiological change is thus increased, the more will it in turn promote the morphological. By such action and reaction the development of each furthers the development of the other, till from an almost imperceptible variety, apparently quite fertile [Pg 55]

with its parent form, there arises a distinct species absolutely sterile with its parent form. In such cases, therefore, it is still the physiological conditions which have *selected* the particular morphological changes capable of so reacting on the reproductive system as to produce cross-infertility, and thus to protect themselves against the destructive power of free intercrossing. So to speak, free intercrossing is always on the watch to level down any changes which natural [Pg 56] selection, or any other cause of varietal divergence, may attempt to produce; and therefore, in order to produce—or to increase—such divergence in the absence of any other form of isolation, natural selection must hit upon such changes of structure, form, or colour, as are so correlated with the reproductive system as to create the physiological isolation that is required.

To show how the principle of selective fertility may be combined with what apparently is the most improbable form of isolation for this purpose—the geographical—I quote the following suggestion made by Professor Lloyd Morgan in his *Animal Life and Intelligence*:—

> Suppose two divergent local varieties were to arise in adjacent areas, and were subsequently (by stress of competition or by geographical changes) driven together into a single area.... If their unions be fertile, the isolation will be annulled by intercrossing —the two varieties will form one mean or average variety. But if the unions be infertile, the isolation will be preserved, and the two varieties will continue separate. Suppose now, and the supposition is by no means an improbable one, that this has taken place again and again in the evolution of species; then it is clear that those varietal forms which had continued to be fertile together would be swamped by intercrossing; while those varietal forms which had become infertile would remain isolated. Hence, in the long run, isolated forms occupying a common area would be infertile, (p. 107.)

If then cross-sterility may thus arise even in association with geographical isolation, may it not also arise in its absence? And may it not thus give rise to the differentiation of varieties on account of this physiological isolation alone?

Only two further points need be mentioned to make this statement of physiological selection as [Pg 57] complete as the present *résumé* of its main principles requires.

The first is, that, as Mr. Wallace remarks, "every species has come into existence coincident both in space and time with a pre-existing and closely allied species." I regard this as important evidence that physiological selection is one of the natural causes concerned. For the general fact implied is that every species has come into existence on an area occupied by its parent type, and therefore under circumstances which render it imperative that intercrossing with that type should be prevented. In the case of monotypic evolution by natural selection alone, intercrossing with the parent type is prevented through the gradual extinction of that type by successive generations of the developing type. But in the case of polytypic evolution, intercrossing with the parent type can only be prevented by some form of isolation other than natural selection; and here it is evident that cross-infertility with the parent type must be as efficient to that end as any other form of isolation that can be imagined. Consequently we might almost have expected beforehand that in a large proportional number of cases cross-infertility should have been the means employed. And the fact that this is actually the case so far corroborates the only theory which is able to explain it.

The second point is this.

It appears to be comparatively rare for any cause of specific divergence to prove effectual on common areas, unless it sooner or later becomes associated with some degree of cross-infertility. [Pg 58] But through this association, the segregating influence of both the causes concerned is, as Mr. Gulick has shown, greatly increased. For instance, if the segregating influence of some degree of cross-infertility be associated with that of any other form of isolation, then, not only will the two segregating influences be added, but multiplied together. And thus, by their mutual action and reaction, divergent evolution is promoted at a rapidly increasing rate.

I will now summarize the main points of the theory of physiological isolation in a categorical form.

1. If no other form of isolation be present, specific divergence can only take place when some degree of cross-infertility has previously arisen between two or more sections of a species.

2. When such cross-infertility has arisen it may cause specific divergence, either (*a*) by allowing independent variability in each of the physiologically isolated groups; (*b*) by becoming associated with any other cause of differentiation already operating; or (*c*) by both these means combined.

3. As some degree of cross-infertility generally obtains between allied species, we are justified in concluding that this has been the most frequent—or, at any rate, the most effective—kind of isolation where the origin of species is concerned; and therefore the kind with which, in the case of species-formation, natural selection, or any other cause of specific divergence, has been most usually associated.

4. Where varietal divergence has begun in the absence of cross-infertility, such divergence [Pg 59] seems, as a general rule, to have been incapable of attaining to a specific value.

5. Therefore, in the vast majority of such cases, it must have been those varietal changes of structure, size, colour, &c., which happened to have afterwards been assisted by the reproductive change that were on this account *selected* as successful candidates for specific differentiation.

6. It follows, that it makes no difference to the general theory of physiological selection in what proportion of cases the physiological change has been the initial change; for, whether prior or subsequent to the varietal changes with which it becomes associated, its presence has been equally important as a condition to specific divergence.

7. When physiological isolation becomes associated with natural selection, or any other form of homogamy, the segregative power of both is augmented. Moreover, so great is the augmentation that even very moderate degrees of physiological isolation—themselves capable of effecting little or nothing—become very powerful when associated with moderate degrees of any other kind of homogamy, and vice versa.

8. The theory of physiological selection effectually explains the divergent evolution of specific types and the cross-infertility of such types when evolved.

To prevent, if possible, the continuance of certain misunderstandings with regard to my original statement of the new theory, let me here disclaim some views which have been assigned to me. They are:

1. That the theory of physiological selection is opposed to the theory of natural selection. Far from this being so, it is—at all events in my own opinion—a very important aid to it, in preventing free intercrossing on a common area, and thus allowing divergent evolution to occur within that area. [Pg 60]

2. That, in advancing the theory of physiological selection as "an additional suggestion on the origin of species," I wish to represent it as being the originating cause of *all* species. What I hold is, that all species must have owed their origin to *isolation*, in some form or other; but that as physiological selection is only one among many other forms of isolation (including natural selection), and as it can only act on common areas, a large number of species must have been formed without its aid.

3. That I imagine physiological varieties always to arise "sporadically," or as merely individual "sports" of the reproductive system. On the contrary, I expressly stated that this is *not* the way in which I suppose the "physiological variation" to arise, when giving origin to a new species; but that it arises, whenever it is effectual, as a "collective variation" affecting a number of individuals simultaneously, and therefore characterizing "a whole race, or strain."

4. That I suppose physiological selection always to act alone. This I have never supposed. The essential point is, not that the physiological isolation is unassociated with other forms of isolation, but that unless associated with some degree of physiological isolation, no one of the other forms is capable of originating species on common areas with any approach to frequency. [Pg 61] This proposition is the essence of the new theory, and I take it to be proved, not only by general deductive reasoning which shows that it *must* be so, but also by the fact of an otherwise inexplicable association between specific divergence on common areas and some more or less considerable degree of mutual infertility.

CHAPTER IV. [Pg 62]

Evidences of Physiological Selection.

I will now give an outline sketch of the evidences in favour of the theory which has been set forth in the preceding chapter, stating first what is the nature of the verification which it requires.

The theory is deduced from a highly general association between distinctive specific characters of *any* kind and a relatively constant specific character of a *particular* kind—namely, sexual exclusiveness. For it is from this highly general association that the theory infers that this relatively constant specific character has been at least one of the needful conditions to the development of the other specific characters with which it is found associated. Hence the necessary verification must begin by showing the strength of the theory on these merely deductive, or antecedent, grounds. It may then proceed to show how far the facts of organic nature corroborate the theory in other and independent ways.

First, let it be carefully observed that here we have to do only with the *fact* of selective fertility, and with its *consequences* as supposed by the theory: we have nothing to do 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 if the needful variations are provided, without its being incumbent on either to explain the causes which produce them. Not with its degrees, because, in the first place, it can only be those degrees of variation which in particular cases are supposed adequate to induce specific divergence, that fall within the scope of the theory; and because, in the second place, degrees which are adequate only to induce—or to assist in inducing, *varietal* divergence, must always tend to increase, or pass into higher degrees. [Pg 63]

Antecedent Standing of the Theory.

The antecedent standing or logical basis of the theory has already been in large measure displayed in the preceding chapter; for it was impossible to state the theory without thereby showing in how considerable a degree it is self-evident. A brief recapitulation is therefore all that is here necessary.

It has been shown that divergent or polytypic evolution on common areas is inexplicable by natural selection alone. Hence the question arises: What form of isolation has, under such circumstances, rendered possible divergent evolution? In answer to this question the theory of physiological selection suggests that variations in the reproductive function occur in such a way as to isolate more or less perfectly from each other different sections of a species. While cross-fertility remains unimpaired among the members of each section, there is more or less cross- [Pg 64]
infertility when members of either section mate with those of the other. Thus a physiological barrier is interposed between the two sections; and any divergences of structure, colouring, or instinct arising in the members of either section will not in any way be affected by such divergences as arise among the members of the other.

In support of this suggestion, it has been shown in the preceding chapter that the very general association of cross-infertility with specific differentiation points most strongly to the inference that the former has usually been an indispensable condition to the occurrence of the latter. It cannot be denied that in many cases the specific distinction is now maintained by means of that sexual isolation which cross-infertility confers: it is therefore probable that such isolation has been instrumental in securing its initial attainment.

This probability is strengthened by the observed fact that the general association in question is conspicuously absent in the case of domesticated varieties, notwithstanding that their multitudinous and diverse varietal characters usually equal, and frequently surpass, specific characters in their degrees of divergence.

Since, then, it would seem to be impossible for divergent evolution on common areas to take place in the absence of some mode of isolation; since cross-infertility appears to be the only possible mode under the given circumstances; and since among domesticated varieties, where isolation is otherwise secured by artificial means, cross-infertility is usually absent, the logical [Pg 65]
foundations of the theory of physiological selection would seem to be securely laid.

We may therefore pass to more special lines of evidence.

Evidence from Geographical Distribution.

Darwin has adduced very good evidence to show that large areas, notwithstanding the disadvantages which (on his theory) must arise from free intercrossing, are what he terms better manufactories of species than smaller areas, such as oceanic islands. On the other hand, as a matter of fact, oceanic islands are comparatively rich in peculiar species. These two statements, however, are not incompatible. Smaller areas are, as a rule, rich in peculiar species relatively to the number of their inhabitants; but it does not follow that they are rich in species as contrasted with larger areas containing very many more inhabitants. Therefore, the rules are that large areas turn out an absolutely greater number of specific types than small areas; although, relatively to the number of individuals or amount of population, the small areas turn out a larger number of species than the large areas.

Now, these two complementary rules admit of being explained as Darwin explains them. Small and isolated areas are rich in species relatively to the amount of population, because, as we have before seen, this population has been permitted to develop an independent history of its own, shielded from intercrossing with parent forms, and from competition with exotic forms; while, at the same time, the homogamy thus secured, combined with change of environment, will give [Pg 66]
natural selection an improved chance of finding new points of departure for its operation. On the other hand, large and continuous areas are favourable to the production of numerous species, first, because they contain a large population, thus favouring the occurrence of numerous variations; and, secondly, because the large area furnishes a diversity of conditions in its different parts, as to food, climate, attitude, &c., and thus so many different opportunities for the occurrence of sundry forms of homogamy. Now, it is obvious that of all these sundry forms of homogamy, physiological selection must have what may be termed a first-rate opportunity of assisting in the manufacture of species on large areas. For not only is it upon large and continuous areas that the antagonistic effects of intercrossing are most pronounced (and, therefore, that the influence of physiological selection must be most useful in the work of species-making); but here also the diversity in the external conditions of life, which the large area supplies to different parts of the extensive population, cannot fail to furnish physiological selection with a greater abundance of that particular variation in the reproductive system on which its action depends. Again, and of still more importance, on large areas there are a greater *number* of species already differentiated from one another as such; thus a greater number of already sexually differentiated forms are presented for further differentiation at the hands of physiological selection. For all these reasons, therefore, we might have expected, upon the new theory, that large and continuous areas would be good manufactories of species.

Again, Darwin has shown that not only large areas, but likewise "dominant" genera within those [Pg 67]
areas, are rich in species. By dominant genera he meant those which are represented by

numerous individuals, as compared with other genera inhabiting the same area. This general rule he explains by the consideration that the qualities which first led to the form being dominant must have been useful; that these would be transmitted to the otherwise varying offspring; and, therefore, that when these offspring had varied sufficiently to become new species, they would still enjoy their ancestral advantages in the struggle for existence. And this, doubtless, is in part a true explanation; but I also think that the reason why dominant genera are rich in species, is chiefly because they everywhere present a great number of individuals exposed to relatively great differences in their conditions of life: or, in other words, that they furnish the best raw material for the manufacture of species by physiological selection, as explained in the last paragraph. For, if the fact of dominant genera being rich in species is to be explained *only* by natural selection, it appears to me that the useful qualities which have already led to the dominance of the ancestral type ought rather to have proved inimical to its splitting up into a number of subordinate types. If already so far "in harmony with its environment" as to have become for this reason dominant, one would suppose that there is all the more reason for its not undergoing change by the process of natural selection. Or, at least, I do not see why the fact of its being in an unusual degree of harmony with its environment should in itself constitute any [Pg 68] unusual reason for its modification by survival of the fittest. On the other hand, as just observed, I do very plainly see why such a reason is furnished for the modifying influence of physiological selection.

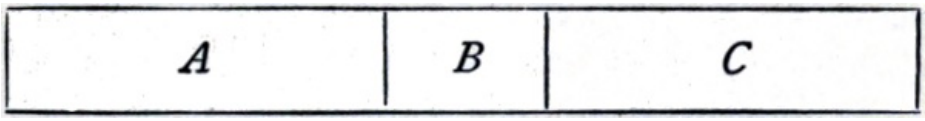
Let us next turn to another of Darwin's general rules with reference to distribution. He took a great deal of trouble to collect evidence of the two following facts, namely, (1) that "species of the larger genera in each country vary more frequently than the species of the smaller genera"; and (2) that "many of the species included within the larger genera resemble varieties in being very closely, but unequally, related to each other, and in having restricted ranges[22]." 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 well-marked adaptive meanings; yet this is precisely what we do not find. For Darwin's argument here is 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 view of this evolution being due solely to natural selection. On the other hand, the argument tells strongly (though unconsciously) [Pg 69] in favour of physiological selection. For the larger a genus, or the greater the number of its species, the greater must be the opportunity for the occurrence of that particular kind of variation on which the principle of physiological selection depends. 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 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 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 as a rule, and in the first instance, determined by changes in the reproductive system, 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.

The two subsidiary facts, that very closely allied species have restricted ranges, and that dominant species are rich in varieties, both seem to tell more in favour of physiological than of natural selection. For "very closely allied species" is but another name for species which scarcely differ from one another at all except in their reproductive systems; and, therefore, the more restricted their ranges, the more certainly would they have become fused by intercrossing with [Pg 70] one another, had it not been for the barrier of sterility imposed by the primary distinction. Or rather, I should say, had it not been for the original occurrence of this barrier, these now closely-allied species could never have become species. Again, that dominant species should be rich in varieties is what might have been expected; for the greater the number of individuals in a species, the greater is the chance of variations taking place in all parts of the organic type, and particularly in the reproductive system, seeing that this system is the most sensitive to small changes in the conditions of life, and that the greater the number of individuals composing a specific type, the more certainty there is of some of them encountering such changes. Hence, the richness of dominant species in varieties is, I believe, mainly due to the greater opportunity which such species afford of some degree of cross-infertility arising between their constituent members.

Here is another general fact, also first noticed by Darwin, and one which he experiences some difficulty an explaining on the theory of natural selection. He says:—

> In travelling from north to south over a continent, we generally meet at successive intervals with closely-allied or representative species, evidently filling the same place in the economy of the land. These representative species often meet and interlock, and as one becomes rarer and rarer, the other becomes more and more frequent, till the one replaces the other. But if we compare these species where they intermingle, they are generally as absolutely distinct from each other in every detail of structure as are specimens taken from the metropolis of each.... In the intermediate region, having [Pg 71]

intermediate conditions of life, why do we not now find closely-linking intermediate varieties? This difficulty for a long time quite confounded me. But I think it can in large part be explained[23].



His explanation is that, "as the neutral territory between two representative species is generally narrow in comparison with the territory proper to each, ... and as varieties do not essentially differ from species, the same rule will probably apply to both; and, therefore, if we take a varying species inhabiting a very large area, we shall have to adapt two varieties to two large areas, and a third variety to a narrow intermediate zone." It is hence argued that this third or intermediate variety, on account of its existing in lesser numbers, will probably be soon overrun and exterminated by the larger populations on either side of it. But how is it possible "to adapt two varieties to two large areas, and a third [transitional] variety to a narrow intermediate zone," in the face of free intercrossing on a continuous area? Let *A*, *B*, and *C* represent the three areas in question. According to the argument, variety *A* passes first into variety *B*, and then into variety *C*, while variety *B* eventually becomes exterminated by the inroads both from *A* and *C*. But how can all this have taken place with nothing to prevent intercrossing throughout the entire area *A*, *B*, *C*? I confess that to me it seems this argument can only hold on the supposition that the analogy between varieties and species extends to the reproductive system; or, in a sense more absolute [Pg 72] than the argument has in view, that "varieties do not essentially differ from the species" which they afterwards form, but from the first show some degree of infertility towards one another. And, if so, we have of course to do with the principles of physiological selection.

That in all such cases of species-distribution these principles have played an important part in the species-formation, appears to be rendered further probable from the suddenness of transition on the area occupied by contiguous species, as well as from the completeness of it—i. e. the absence of connecting forms. For these facts combine to testify that the transition was originally due to that particular change in the reproductive systems of the forms concerned, which still enables those forms to "interlock" without intercrossing. On the other hand, neither of these facts appears to me compatible with the theory of species-formation by natural selection alone.

But this leads us to another general fact, also mentioned by Darwin, and well recognized by all naturalists, namely, 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. Now, the large body of facts to which I here allude, but need not at present specify, appear to me to constitute one of 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 [Pg 73] those on either side of it by the minute and trivial distinctions of a secondary kind, but all the links of which differ from one another in respect of the primary distinction, 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 secondary distinctions, distributed as they are over different parts of all these kindred organisms, and yet nowhere presenting any but a trifling amount of morphological change?

For my own part, I cannot believe—any more than Darwin could believe—that all these numerous, diverse, and trivial changes have always had the accidental effect of inducing the same peculiar change in the reproductive system, and so producing it without any reference to the process of specific divergence. Nor can I believe, as Darwin incidentally and provisionally suggested, that prolonged exposure to uniform conditions of life have so generally induced an equally meaningless result. I can only believe that all the closely allied species inhabiting our supposed continent, and differing from one another in so many and such divers points of small detail, are merely so many records of the fact that selective fertility has arisen among their ancestry, and has thus given as many opportunities for the occurrence of morphological differentiations as it has furnished cases of efficient isolation. Of course, I do not deny that many, or probably most, of these trivial morphological differentiations have been produced by natural selection on account of their utility: I merely deny that they could have been so produced on this [Pg 74] common area, but for the sexual isolation with which every distinct set of them is now found to be associated.

Evidence from Topographical Distribution of Species.

By topographical distribution I mean the distribution of organisms with reference to comparatively small areas, as distinguished from larger regions with reference to which the term geographical distribution is appropriate.

It will be at once apparent that a study of the topographical distribution of organic types is of even more importance for us than a study of their geographical distribution. For while the former study is conducted, as it were, with a low power of our observing microscope, the latter is conducted with a high power. The larger facts of geographical distribution yield, indeed, all the general characters which we might expect them to yield, on the theory that divergence of specific types on common areas has been in chief part determined by physiological conditions. But for the

purpose of testing this theory in a still more exacting manner, it is of the first importance to consider the more detailed facts of topographical distribution, since we here come to closer quarters with the problem of specific differentiation. Therefore, as we have already considered this problem under the most general points of view, we will now consider it under more special points of view.

It is self-evident, as we have seen in the preceding section, that the greater the number of [Pg 75] individuals of the same species on a given area, the less must be the power of natural selection to split that species into two or more allied types; because, the more crowded the population, the greater must be the uniformitarian effect of free intercrossing. This obvious fact has been insisted upon by several previous writers on Darwinism; and the only reason why it has not been recognized by all naturalists is that so few of them have observed the all-important distinction between monotypic and polytypic evolution. The denser the population, and therefore the greater the intercrossing and the severer the struggle for existence within the species, the better will it be for *transmutation* of the species by natural selection; but the worse it will be for *differentiation* of the species by this form of homogamy. On the other hand, if physiological selection be entertained as a form of homogamy, the denser the population, the better opportunity it will have of differentiating the species, first, because a greater number of individuals will be present in which the physiological change may arise, and, secondly, because, if it does arise, the severity of the struggle for existence will *then* give natural selection a better chance of acting rapidly and effectually on each of the isolated sections.

Hence, where the question is whether selective fertility has played any large or general part in the differentiation of specific types, the best criterion we can apply is to ascertain whether it is a general rule that closely allied species occur in intimate association, so that their individual members constitute, as it were, a single population, or, on the other hand, whether they occur [Pg 76] rather on different sides of physical barriers. If they occur intimately associated, the form of homogamy to which their differentiation was due must have presumably been the physiological form; whereas, if they are proved to be correlated with physical barriers, the form of homogamy which was concerned in their differentiation must presumably have been the geographical form.

Now, at first this consideration was a trouble to me, because Moritz Wagner had strenuously argued—and supported his argument by a considerable wealth of illustration—that allied species are always found correlated with physical barriers or discontinuous areas. Weismann's answer, indeed, had shown that Wagner's statement was much too general: nevertheless, I was disappointed to find that so much could be said in favour of the geographical (or topographical) form of isolation where closely allied species are concerned. Subsequently, however, I read the writings of Nägeli on this subject, and in them I find a very different state of matters represented.

Seeing as clearly as Wagner that it is impossible under any circumstances for natural selection to cause specific *differentiation* unless assisted by some other forms of homogamy, but committing the same oversight as Wagner and Weismann in supposing that the only other form of homogamy in nature is geographical isolation, Nägeli, with great force of reasoning, and by many examples, founded his argument against the theory of natural selection on the ground that in the vegetable kingdom closely allied species are most frequently found in intimate association with one [Pg 77] another, not, that is to say, in any way isolated by means of physical barriers. This argument is everywhere logically intact; and, as he sustains it by a large knowledge of topographical botany, his indictment against natural selection as a cause of specific *differentiation* appeared to be insurmountable. And, in point of fact, it *was* insurmountable; so that the whole problem of the origin of species by *differentiation on common areas* has hitherto been left in utter obscurity. Nor is there now any escape from this obscurity, unless we entertain the "supplementary factor" of selective fertility. And, apparently, the only reason why this has not been universally recognized, is because Darwinians have hitherto failed to perceive the greatness of the distinction between the *differentiation* and the *transmutation* of species; and hence have habitually met such overwhelming difficulties as Nägeli presented by an illogical confounding of these two totally distinct things.

But if the idea of selective fertility had ever occurred to Nägeli as a form of segregation which gives rise to specific differentiation, I can have no doubt that so astute and logical a thinker would have perceived that his whole indictment against natural selection was answered. For it is incredible that he should not have perceived how this physiological form of homogamy (supposing it to arise *before* or *during*, and not *after* the specific differentiation) would perform exactly the same function on a continuous area, as he allowed that "isolation" does on a discontinuous one.

However, be this as it may, there cannot be any question touching the immense value of his facts [Pg 78] and arguments as evidence in favour of physiological selection—albeit this evidence was given unconsciously, or, as it were, prophetically. Therefore I will here quote a few examples of both, from his paper *Du Développement des Espèces Sociales*[24].

After stating the theory of natural selection, he says that if the theory is (of itself) a true explanation of the origin (or divergence) of specific forms, it ought to follow that

> two closely allied forms, derived the one from the other, would necessarily occupy two

> different geographical areas [or topographical stations], since otherwise they would soon become blended. Until they had already become sufficiently consolidated as distinct species to render mutual intercrossing highly improbable, they could not be intermingled without disadvantage [to differentiation]. Had Darwin endeavoured to support his hypothesis by facts, he would, at least in the vegetable kingdom, have found little to favour his cause. I can cite many hundreds of cases, in which species in every stage of development have been found closely mingling with one another, and not in any way isolated. Therefore, I do not think that one can rightly speak of natural selection in the Darwinian sense in the vegetable kingdom; and, in my estimation, there is a great difference between the formation of species by nature and the production of stock by a breeder.... (p. 212).
>
> Of the two kinds of distribution (i. e. growing apart and growing together), Synoicy (or growing together) is by far the most usual in nature. I reckon that out of a hundred allied vegetable forms, at least ninety-five would be found to be synoical (p. 219).

This is a most important point. That so enormous a proportion of vegetable species should have originated in intimate association with their parent or sister types, is clearly unintelligible on the theory of natural selection alone; there obviously *must* be some other form of homogamy which, whether or not in all places *associated* with natural selection, is the primary condition to the differentiation. Such I hold with Nägeli, is a logical necessity; and this whether or not I am right in believing the other form of homogamy in question to be selective fertility. But I go further and say, Surely there can be no rational question that this other form of homogamy must have been, at any rate as a highly general rule, the one which I have assigned. For how is it that in these ninety-five per cent. of cases, where vegetable species are growing intimately associated with their nearest allies, there is no hybridizing, or blending and relapsing to the original undifferentiated types? We know well the answer. These are fully differentiated species, and, as such, are protected from mutual intercrossing by the barrier of mutual sterility. But now, if this bar is thus necessary for preserving the specific distinctions when they have been fully developed, much more must it have been so to admit of their development; or, otherwise stated, since we know that this barrier is associated with "synoical" species, and since we clearly perceive that were it withdrawn these species would soon cease to exist, can we reasonably doubt that their existence (or origin) is due to the previous erection of this barrier? If synoical species were comparatively rare, the validity of such reasoning might be open to question; or, even if we should not doubt it in such cases, at any rate we might well doubt the importance or extent of selective fertility as a factor in the origination of species. But the value of Nägeli's writings on the present subject consists in showing that synoical species constitute so overwhelming a majority of the vegetable kingdom, that here, at all events, it appears impossible to rate too highly the importance of the principle I have called physiological selection.

[Pg 79]

[Pg 80]

CHAPTER V.

[Pg 81]

Further Evidences of Physiological Selection.

Evidence from Topographical Distribution of Varieties.

In the last section we have considered the topographical distribution of closely allied *species*. I now propose to go still further into matters of detail, by considering the case of natural *varieties*. And here we come upon a branch of our inquiry where we may well expect to meet with the most crucial tests of our theory. For if it should appear that these nascent species more or less resemble fully developed species in presenting the feature of cross-infertility, the theory would be verified in the most direct and conclusive manner possible. These nascent species may be called embryo species, which are actually in course of differentiation from their parent-type; and therefore, if they do not exhibit the feature in relation to that type which the present theory infers to be necessary for the purposes of differentiation, the theory must be abandoned. On the other hand, if they do exhibit this feature, it is just the feature which the theory predicted as one that would be found highly characteristic of such embryo types. Contrariwise, the theory of natural selection can have no reason to form any such anticipation; or rather its anticipation would necessarily require to be the exact opposite. For, according to this theory, the cross-infertility of allied species is due, either to correlation with morphological changes which are being produced by the selection, or else, as Darwin supposed, to "prolonged exposure to uniform conditions of life"; and thus, in either case, the sterility variation ought to be, as a general rule at all events, subsequent to the specific differentiation, and, according to Darwin's view, *long* subsequent. Thus we ought not to find that the physiological change is ever, on any large or general scale, the initial change; nor ought we to find that it is, on any such scale, even so much as a contemporary change: there ought, in fact, to be no constant or habitual association between divergence of embryo-types and the concurrence of cross-infertility.

[Pg 82]

Now, it will be my endeavour to prove that there is an extraordinarily general association between *varietal* divergence and cross-infertility, *wherever common areas are concerned*; and in as far as this can be proved, I take it that the evidence will make wholly in favour of physiological selection as the prime condition to specific divergence, while at the same time they will make no less wholly, *and quite independently*, against natural selection as the unaided cause of such

divergence.

I shall begin with some further quotations from Nägeli.

> Species may be synoical at all stages of relationship. We come across varieties, scarcely distinguishable from one another, growing in the same locality (as, for example, the *Cirsium heterophyllum*, with smooth or jagged leaves, the *Hieracium sylvaticum*, with or without caulinary leaves); again, we meet other varieties more accentuated (as the *H. hoppeanum*, with under ligules of white or red, the *Campanula*, with white or lilac flowers, &c.), other varieties even more marked, which might almost be elevated to the rank of species (*Hieracium alpinum*, with hairs and glands, and the new form *H. holadenium*, which has only glands, *Campanula rotundifolia* with smooth and hairy leaves), or forms still more distinct, up to well-defined species. I could enumerate endless examples at all stages. [Pg 83]
>
> It will be seen that in my definition of synoicy I do not mean to assert that *all* allied forms are invariably found together, but that they are much more often seen in groups than singly. Take, for instance, nine forms closely related (*A* to *I*). *A*, *E*, *H* will be found side by side at one point, *B*, *D* at another, *C*, *F* at a third, &c. These facts are plainly opposed to the theory of isolation and amixia, and make, on the contrary, in favour of the social development of species (*loc. cit.*, p. 221).

Not to multiply quotations to the same general effect, I will supply but one other, referring to a particular case.

> At one spot (*Rothwand*) much exposed to the sun, and difficult of access, I remarked two closely allied forms, so nearly related to *H. villosum* that this would seem to be an intermediary form between the two. One of these (*H. villosissimum*) is distinguished by its tongue and thick pubescence, its tolerably large capitula, and by the lengthened and separated scales of the involucrum; the other, on the contrary (*H. elongatum*), is less pubescent, has smaller capitula, and more compact scales on the involucrum than *H. villosum*. Both are finally distinguishable from the type by their longer stalks, which are more decidedly aphyllous, and by their later flowering. At the spot where I found them the two forms were closely intermingled, and each was represented by a considerable number of plants. I did not find them anywhere else on the mountain, nor could I find at the spot where these were growing a single specimen of the true *H. villosum*, nor a single hybrid from these two.
>
> I concluded that these two new forms had, by joining their forces, expelled the *H. villosum* from its primitive abode, but had not succeeded in displacing one another. As to their origin, they had evidently developed in two different directions from a common point of departure, namely *H. villosum*. They had succeeded, not only in separating themselves from the original form, but also in preventing any intermediary form from interposing. I thought myself therefore justified in considering this as a case of varieties which have come into existence subsequently to the Glacial epoch. The morphological characteristics of the three forms are sufficiently distinct for them to be designated as species by a good many writers. They are better defined than some of MM. Frolich and Fries' weaker species, and as well defined as some of MM. Koch and Grisebach's (p. 222). [Pg 84]

Now it is clear, without comment, that all this is exactly as it ought to be, if allied species have been differentiated on common areas by selective fertility. For if, as Nägeli elsewhere says, "one meets forms in nature associated with one another, and severally distinguished by every possible degree of differentiation," not only as Nägeli adds, does this general fact lead to the inference that species are (usually) developed when plants grow intimately associated together; but as certainly it leads to the further inference that such development must be due to a prior development of cross-infertility between the diverging varietal forms, cross-infertility which is therefore afterwards so characteristic of the allied species, when these are found, in their fully differentiated condition, still occupying the same area in large and intimately mingled populations.

To my mind there could not be any inference more strongly grounded than this, because, with the one exception of the physiological form, no other form of homogamy can be conceived which shall account for the origin and permanence of these synoical varieties, in all degrees of differentiation up to well-defined synoical species. Least of all, as we have seen, can natural selection alone have had anything to do with such a state of matters; while, as we have likewise seen, in all its details it is exactly the state of matters which the theory of physiological selection requires. [Pg 85]

Nevertheless, although this inference is so strongly grounded, we ought to remember that it is only an inference. In order fully to verify the theory of physiological selection, we ought to prove by experiment the fact of cross-infertility between these synoical varieties, as we learn that it afterwards obtains between synoical species. It is to be regretted that the theory of physiological selection did not occur to the mind of Nägeli, because he would then, no doubt, have ascertained this by actual experiment. As it is, the great value of his observations goes no further than establishing a strong presumption, that it *must* be selective fertility which causes the progressive differentiation of synoical varieties; and also that, if so, this *must* be the principal factor in the

differentiation of vegetable species, seeing that some ninety-five per cent. are of synoical origin.

Evidence from Experimental Research.

My paper on *Physiological Selection* pointed out that the whole theory would have to stand or fall with the experimental proof of the presence or the absence of cross-infertility between varieties of the same species growing on common areas. From the facts and considerations which we have hitherto been dealing with, it did indeed appear to me that there was the strongest conceivable [Pg 86] ground for inferring that cross-infertility between such varieties would be found by experiment to be a phenomenon of highly general occurrence—amply sufficient ground to prove that allied species on common areas for the most part owed their origin to this character of mutual sterility, and not vice versa as previously supposed. At that time I was not aware that any experiments had been made in this direction. Soon after the paper was published, however, my attention was directed to a laborious research which had been directed to this very point, and carried on for more than thirty years, by M. Jordan[25]. This had not attracted the general notice which it undoubtedly deserved; and I have since ascertained that even Darwin began to look into it only a few months before his death.

Having devoted his life to closely observing in divers stations multitudes of different species of plants—annuals and perennials, bulbous and aquatic, trees and shrubs—M. Jordan has been able to satisfy himself, and the French school of botanists to which this line of observation has given rise, that in most cases (or "nearly everywhere"), when a Linnean species is indigenous to a country and is there of common occurrence, this species within that district is represented by more or less numerous and perfectly constant varieties. These varieties are constituted by such minute differences of morphological character that their very existence eluded the observation of [Pg 87] botanists, until M. Jordan began to search specially for them as the special objects of his scrutiny. Moreover, these varieties of a Linnean species occupy common areas, and there grow in intimate association with one another, or as M. Jordan says, "*pêle-mêle*." So far, be it noticed, Jordan was proceeding on exactly the same lines as Nägeli; only he carried his observations over a still wider range of species on the one hand, and into a still minuter search for varieties on the other. But the all-important point for us is, that he further proceeded to test by experiment the physiological relations between these morphological varieties; and found, in many hundreds of cases, that they not only came true to seed (i. e. are hereditary and not merely climatic), but likewise cross-sterile *inter se*. For these reasons, M. Jordan, who is opposed to the theory of evolution, regards all such varieties as separately created species; and the inspiring motive of his prolonged investigations has been a desire to multiply these proofs of creative energy. But it clearly makes no difference, so far as evolutionists are concerned with them, whether all this multitude of sexually isolated forms be denominated species or varieties.

The points which are of importance to evolutionists—and of the first order of importance in the present connexion—may be briefly summarized as follows:—

(1) The research embraces large numbers of species, belonging to very numerous and very varied orders of plants; (2) in the majority of cases—although not all—indigenous species which are of common occurrence present constant varieties; (3) these varieties, nevertheless, may be [Pg 88] morphologically so slight as to be almost imperceptible; (4) they occupy common areas and grow in intimate association; (5) although many of them have undergone so small an amount of morphological change, they have undergone a surprising amount of physiological change; for (6) not only do very many of these varieties come true to seed; but, (7) when they do, they are always more or less cross-infertile *inter se*.

Now, it is self-evident that every one of these seven points is exactly what the theory of physiological selection requires, while there is not one of them which it does not require. For if the theory be sound, we should expect to find large numbers of species belonging to numerous and varied orders of plants presenting constant varieties on common areas; we should expect this to be a highly general, though not a universal, rule; and we should expect it to apply only to species which are indigenous. Moreover, we should expect these varieties, although but slightly differentiated morphologically, to present a great differentiation physiologically—and this in the special direction of selective fertility, combined, of course, with heredity.

On the other hand, as I have said, this catalogue of evidences leaves nothing to be supplied. It gives us all the facts—and no more than all the facts—which my paper on *Physiological Selection* anticipated as the eventual result of a prolonged experimental research. And if I have to regret my ignorance of these facts when that paper was published, at any rate it now furnishes the best proof that my anticipations were not guided by the results of a verification which had already [Pg 89] been supplied. These anticipations were deduced exclusively from the theory itself, as representing what *ought* to be the case if the theory were true; and, I must confess, if I had then been told that they had already been realized—that it had actually been found to be a general rule that endemic species present constant and hereditary varieties, intimately commingled on common areas, morphologically almost indistinguishable, but physiologically isolated by selective fertility—I should have felt that the theory had been verified in advance. For there are only two alternatives: either these things are due to physiological selection, or else they are due—as M. Jordan himself believes—to special creation. Which is equivalent to saying that, for evolutionists, the facts must be held to verify the former theory in as complete a manner as it is logically possible for the theory to be verified.

Evidence from Prepotency.

We have now to consider the bearing of what is called "prepotency" on the theory of physiological selection.

Speaking of the vast number of species of Compositae, Darwin says:—

> There can be no doubt that if the pollen of all these species could be simultaneously or successively placed on the stigma of any one species, this one would elect with unerring certainty its own pollen. This elective capacity is all the more wonderful, as it must have been acquired since the many species of this great group of plants branched off from a common progenitor.

Darwin is here speaking of elective affinity in its fully developed form, as absolute cross-sterility between fully differentiated species. But we meet with all lower degrees of cross-infertility— [Pg 90] sometimes between "incipient species," or permanent varieties, and at other times between closely allied species. It is then known as "prepotency" of the pollen belonging to the same variety or species over the pollen of the other variety or species, when both sets of pollen are applied to the same stigma. Although in the absence of the prepotent pollen the less potent will fertilize the seed, yet, such is the appetency for the more appropriate pollen, that even if this be applied to the stigma some considerable time after the other, it will outstrip or overcome the other in fertilizing the ovules, and therefore produce the same result on the next generation as if it had been applied to the mother plant without any admixture of the less potent pollen, although in some cases such incipient degrees of cross-infertility are further shown by the number or quality of the seeds being fewer or inferior.

Now, in different varieties and in different allied species, all degrees of such prepotency have been noticed by many observers, from the faintest perceptible amount up to complete impotency of the alien pollen—when, of course, there is absolute sterility between the two varieties or allied species. The inference is obvious. In this graduated scale of prepotency—beginning with an experimentally almost imperceptible amount of sexual differentiation between two varieties, and ending in an absolute partitioning of two allied species—we have the only remaining fact that is [Pg 91] required to complete the case in favour of the present theory. We are here brought back to the very earliest stages of physiological differentiation or to the stages which lie behind Jordan's "Physiological Species"; and therefore, when taken in conjunction with his results, the phenomena of prepotency may be said to give us the complete and final demonstration of one continuous development, which, beginning in an almost imperceptible amount of cross-infertility, ends in absolute cross-sterility. The "elective capacity" to which Darwin alludes as having been "acquired" by all the species of Compositae since they "branched off from a common progenitor," is thus seen among innumerable other species actually in process of acquisition; and so we can perfectly well understand, what is otherwise unintelligible, that closely allied species of plants occur, in ninety-five per cent. of cases, intimately associated on common areas, while exhibiting towards one another the character of mutual sterility.

But more than this. The importance of the widespread phenomena of prepotency to the theory of physiological selection does not consist merely in thus supplying the last link in the chain of evidence touching the origin of species by selective fertility, or "elective capacity." These phenomena are of further importance as showing how in plants, at all events, physiological selection appears to be frequently capable of differentiating specific types without the necessary assistance of any other form of homogamy. In my original statement of the theory, I was careful to insist upon the great value, as differentiating agents, of even small degrees of other forms of homogamy when co-operating with physiological selection. But I also stated my belief that in [Pg 92] many cases selective fertility is presumably of itself capable of splitting a specific type; and the reason why I still believe this is, that I do not otherwise understand these phenomena of prepotency. I cannot believe that in all the innumerable cases where they arise, they have been super-induced by some prior morphological changes going on in some other part of the organism, or by "prolonged exposure to uniform conditions of life," on the part of two well-nigh identical forms which have arisen intimately commingled in exactly the same environment, and under the operation of a previously universal intercrossing. Even if such a thing could be imagined as happening occasionally, I feel it difficult to imagine that it can happen habitually, and yet this view must be held by those who would attribute prepotency to natural selection.

It must never be forgotten that the relatively enormous changes as to size, structure, habit, &c., which are presented by our domesticated plants as results of artificial selection, do not entail the physiological character of cross-sterility in any degree, save possibly in some small number of cases. Although in wild species any correspondingly small percentage of cases (where natural selection happens to hit upon parts of the organism modifications of which produce the physiological change by way of correlation) would doubtless be the ones to survive on common areas, still it is surely incredible that such an accidental association between natural selection and cross-infertility is so habitually the means of specific differentiation as the facts of prepotency (together with the observations of Jordan and Nägeli) would necessarily demand. [Pg 93]

Moreover, this view of the matter is still further corroborated by certain other facts and considerations. For example, the phenomena of prepotency (whether as between varieties or between closely allied species) are found to occur when the two forms occupy a common area, i.e. are growing intermingled with one another. Therefore, but for this physiological differentiation, there could be absolutely nothing to prevent free intercrossing. Yet the fact that

hybrids are so comparatively rare in a state of nature—a fact which Sir Joseph Hooker has pointed out to me as otherwise inexplicable—proves the efficacy of even a low degree of such differentiation in preventing the physiologically-differentiated forms from intercrossing. Even in cases where there is no difficulty in producing artificial hybrids or mongrels between species or varieties growing on common areas, it is perfectly astonishing what an extremely small percentage of the hybrid or mongrel forms are found to occur in nature. And there can be no question that this is due to the very efficient manner in which prepotency does its work—efficient, I mean, from the point of view of the new theory; for upon any other theory prepotency is a meaningless phenomenon, which, notwithstanding its frequent occurrence, plays no part whatever in the process of organic evolution.

I attach considerable importance to the phenomena of prepotency in view of the contrast which is presented between plants and animals in the relation of their species to physical barriers. For animals—and especially the higher animals—appear to depend for their specific differentiations [Pg 94] upon such barriers much more than in the case with plants. This is no more than we should expect; for, in accordance with our theory, selective fertility is not so likely to work alone in the case of the higher animals which mate together, as in plants which are fertilized through the agency of wind or insects. In the former case there is no opportunity given for the first rise of cross-infertility, in the form of prepotency; and even where selective fertility has gained a footing in other ways, the chances against the suitable mating of "physiological complements" must be much greater than it is in the latter case. Hence, among the higher animals, selective fertility ought much more frequently to be found in association with other forms of homogamy than it is among plants. And this is exactly what we find. Thus it seems to me that this contrast between the comparative absence and presence of physical barriers, where allied species of plants and of higher animals are respectively concerned, is entitled to be taken as a further corroboration of our theory. For while it displays exactly such a general correlation as this theory would expect, the correlation is one which cannot possibly be explained on any other theory. It is just where physiological selection can be seen to have the best opportunity of acting (viz. in the vegetable kingdom) that we find the most unequivocal evidence of its action; while, on the other hand, it is just where it can be seen to have the least opportunity of asserting itself (viz. among the higher animals) that we find it most associated with, and therefore assisted by, other forms of homogamy, i. e. not only geographical isolation, but also by sexual preference in pairing, and the [Pg 95] several other forms of homogamy, which Mr. Gulick has shown to arise in different places as the result of intelligence.

Evidence from Special Cases.

Hitherto I have been considering, from the most general point of view, the most widespread facts and broadest principles which serve to substantiate the theory of physiological selection. I now pass to the consideration of one of those special cases in which the theory appears to have been successfully applied.

Professor Le Conte has adduced the fossil snails of Steinheim as serving to corroborate the theory of physiological selection[26].

The facts are these. The snail population of this lake remain for a long time uniform and unchanged. Then a small percentage of individuals suddenly began to vary as regards the form of their shells, and this in two or three directions at the same time, each affected individual, however, only presenting one of the variations. But after all these variations had begun to affect a proportionally large number of individuals, some individuals occur in which two or more of the variations are blended together, evidently, as Weismann says, by intercrossing of the varieties so blended. Later still, both the separate varieties and their blended progeny became more and more numerous, and eventually a single blended type, comprising in itself all the initial varieties, supplanted the parent form. Then another long period of stability ensued until another eruption [Pg 96] of new variations took place; and these variations, after having affected a greater and greater number of individuals, eventually blended together by intercrossing and supplanted their parent form. So the process went on, comparatively short periods of variation alternating with comparatively long periods of stability, the variations, moreover, always occurring suddenly in crops, then multiplying, blending together, and in their finally blended type eventually supplanting their parent form.

Now, the remarkable fact here is that whenever the variations arose, they only intercrossed between themselves, they did not intercross with their parent form; for, if they had, not only could they never have survived (having been at first so few in number and there having been no geographical barriers in the small lake), but we should have found evidence of the fact in the half-bred progeny. Moreover, natural selection can have had nothing to do with the process, because not only are the variations in the form of the shells of no imaginable use in themselves; but it would be preposterous to suppose that at each of these "variation periods" several different variations should always have occurred simultaneously, all of which were of some hidden use, although no one of them ever occurred during any of the prolonged periods of stability. How, then, are we to explain the fact that the individuals composing each crop of varieties, while able to breed among themselves, never crossed with their parent form? These varieties, each time that they arose, were intimately commingled with their parent form, and would certainly have [Pg 97] been reabsorbed into it had intercrossing in that direction been possible. With Professor Le Conte, therefore, I conclude that there is only one conceivable answer to this question. Each crop of varieties must have been *protected from intercrossing with their parent form*.

They must have been the result of a variation, which rendered the affected individuals sterile with their parent form, whilst leaving them fertile amongst themselves. The progeny of these individuals would then have dispersed through the lake, physiologically isolated from the parent population, and especially prone to develop secondary variations as a direct result of the primary variation. Thus, as we might expect, two or three variations arose simultaneously, as expressions of so many different lines of family descent from the original or physiological variety; these were everywhere prevented from intercrossing with their parent form, yet capable of blending whenever they or their ever-increasing progeny happened to meet. Thus, without going into further details, we are able by the theory of physiological selection to give an explanation of all these facts, which otherwise remain inexplicable.

In view of the evidence which has now been presented, I will now ask five questions which must be suitably answered by critics of the theory of physiological selection.

1. Can you doubt that the hitherto insoluble problem of inter-specific sterility would be solved, supposing cross-infertility were proved to arise before or during the process of specific differentiation, instead of after that process had been fully completed? [Pg 98]

2. Can you doubt, after duly considering the circumstances under which allied species of plants have been differentiated—viz. in ninety-five per cent. of cases intimately commingled on common areas, and therefore under identical environments—that cross-infertility *must* have arisen before or during the specific differentiation?

3. Can you doubt, after duly considering the facts of prepotency on the one hand and those of Jordan's physiological varieties on the other, that cross-infertility *does* arise before or during the specific differentiation?

4. If you cannot express a doubt upon any of these points, can you explain why you refuse to accept the theory of the origin of species by means of physiological selection, together with the explanation which this theory affords of the continued cross-fertility of domesticated varieties?

5. Supposing this theory to be true, can you conceive of any other classes of facts which, either quantitatively or qualitatively, could more directly or more effectually prove its truth than those which have now been adduced?

On these five heads I entertain no doubt. I am convinced that the theory of physiological selection is the only one that can explain the facts of inter-specific sterility on the one hand, and, on the other hand, the contrast which these facts display to the unimpaired fertility of our domesticated varieties.

In conclusion, it seems desirable once more to insist that there is no antagonism or rivalry between the theories of natural and of physiological selection. For which purpose I will quote the final paragraph of my original paper. [Pg 99]

> So much, then, for the resemblances and the differences between the two theories. It only remains to add that the two are complementary. I have already shown some of the respects in which the newer theory comes to the assistance of the older, and this in the places where the older has stood most in need of assistance. In particular, I have shown that segregation of the fit entirely relieves survival of the fittest from the difficulty under which it has hitherto laboured of explaining why it is that sterility is so constantly found between species, while so rarely found between varieties which differ from one another even more than many species; why so many features of specific distinction are useless to the species presenting them; and why it is that incipient varieties are not obliterated by intercrossing with parent forms. Again, we have seen that physiological selection, by preventing such intercrossing, enables natural selection to promote diversity of character, and thus to evolve species in ramifying branches instead of in linear series—a work which I cannot see how natural selection could possibly perform unless thus aided by physiological selection. Moreover, we have seen that although natural selection alone could not induce sterility between allied types, yet when this sterility is given by physiological selection, the forms which present it would be favoured in the struggle for existence; and thus again the two principles are found playing, as it were, into each other's hands. And here, as elsewhere, I believe that the co-operation enables the two principles to effect very much more in the way of species-making than either of them could effect if working separately. 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, and 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. [Pg 100]

CHAPTER VI.

A Brief History of Opinions on Isolation as a Factor of Organic Evolution.

[Pg 101]

This historical sketch must begin with a consideration of Darwin's opinions on the subject; but as these were considerably modified from time to time during a period of thirty years by the publications of other naturalists, it will be impossible to avoid cross-references as between his writings and theirs. It may also be observed that the *Life and Letters of Charles Darwin* was not published until the year 1887, so that the various opinions which I shall quote from the letters, and which show some considerable approximation in his later years to the views which have been put forward by Mr. Gulick and myself, were not before us at the time when our papers were read.

The earliest allusion that I can find to geographical isolation in the writings of Darwin occurs in a correspondence with Sir Joseph Hooker, as far back as 1844. He there says:—

> I cannot give my reasons in detail; but the most general conclusion which the geographical distribution of all organic beings appears to me to indicate is, that [Pg 102] isolation is the chief concomitant or cause of the appearance of *new* forms (I well know there are some staring exceptions)[27].

And again:—

> With respect to original creation or production of new forms, I have said that isolation appears the chief element[28].

Next, in the earlier editions of the *Origin of Species* this view is abandoned, and in its stead we meet with the opinion that geographical isolation lends a certain amount of assistance to natural selection, by preventing free intercrossing. But here we must note two things. First, the distinction between monotypic and polytypic evolution is not defined. Secondly, the levelling effect of free intercrossing in nature, and hence its antagonism to divergence of character by natural selection, is not sufficiently recognized; while, on the other hand, and in consequence of this, the importance of isolation as a factor of evolution is underrated—not only in its geographical, but likewise in all its other forms.

Taking these two points separately, the only passages in Darwin's writings, so far at least as I can find, in which any distinction is drawn between evolution as monotypic and polytypic, are those in which he deals with a somewhat analogous distinction between artificial selection as intentional and unconscious. He says, for example:—

> In the case of methodical selection, a breeder selects for some definite object, and if the individuals be allowed freely to intercross, his work will completely fail. But when many men, without intending to alter the breed, have a nearly common standard of [Pg 103] perfection, and all try to procure and breed from the best animals, improvement surely but slowly follows from this unconscious process of selection, notwithstanding that there is no separation of selected individuals. Thus it will be under nature[29].

Here we have what may perhaps be regarded as a glimmering of the distinction between monotypic and polytypic evolution. But that it is only a glimmering is proved by the immediately ensuing sentences, which apply this analogy of unconscious selection *not* to the case of monotypic, *but* to that of polytypic evolution. So likewise, in the succeeding discussion on "divergence of character," the analogy is again resorted to for the purpose of showing how polytypic evolution may occur in nature.

Thus far, then, it may be said that we have scarcely so much as a glimmering of the distinction between monotypic and polytypic evolution; and as the same discussion (with but a few verbal alterations) runs through all the editions of the *Origin*, it may well be asked why I should have alluded to such passages in the present connexion. Well, I have done so because it is apparent that, during the last years of his life, the distinction between selection as "methodical" and "unconscious" enabled Darwin much more clearly to perceive that between evolution as monotypic and polytypic. Thus in 1868 he wrote to Moritz Wagner (who, as we shall presently see, entirely failed to distinguish between monotypic and polytypic evolution), expressing his belief—

> That in many large areas all the individuals of the same species have been slowly modified, in the same manner, for instance, as the English racehorse has been improved, that is, by the continued selection of the fleetest individuals, without any [Pg 104] separation. But I admit that by this process two or more new species could hardly be formed within the same limited area[30].

Again, in 1876 he wrote another letter to Wagner, in which the following passage occurs:—

> I believe that all the individuals of a species can be slowly modified within the same district, in nearly the same manner as man effects by what I have called the process of unconscious selection. I do not believe that one species will give birth to two or more

new species as long as they are mingled together within the same district[31].

Two years later he wrote to Professor Semper:—

> There are two different classes of cases, it appears to me, viz. those in which species becomes slowly modified in the same country, and those cases in which a species splits into two, or three, or more new species; and, in the latter case, I should think nearly perfect separation would greatly aid in their "specification," to coin a new word[32].

Now, these passages show a very much clearer perception of the all-important distinction between monotypic and polytypic evolution than any which occur in the *Origin of Species*; and they likewise show that he was led to this perception through what he supposed to be a somewhat analogous distinction between "unconscious" and "methodical" selection by man. The analogy, I need hardly say, is radically unsound; and it is a curious result of its unsoundness that, whereas in the *Origin of Species* it is adduced to illustrate the process of polytypic evolution, as previously remarked, in the letters above quoted we find it adduced to illustrate the process of [Pg 105] monotypic evolution. But the fact of this analogy being unsound does not affect the validity of the distinction between monotypic and polytypic evolution to which it led Darwin, in his later years, so clearly to express[33].

Turning next to the second point which we have to notice, it is easy to show that in the earlier editions of his works Darwin did not sufficiently recognize the levelling effects of free intercrossing, and consequently failed to perceive the importance of isolation (in any of its forms) as a factor of organic evolution. This may be most briefly shown by quoting his own more matured opinion upon the subject. Thus, with reference to the swamping effects of intercrossing, he wrote to Mr. Wallace in 1867 as follows:—

> I must have expressed myself atrociously: I meant to say exactly the reverse of what you have understood. F. Jenkin argued in the *North British Review* against single variations being perpetuated, and has convinced me, though not in quite so broad a manner as here put. I always thought individual differences more important; but I was blind, and thought that single variations might be preserved much oftener than I now see is possible or probable. I mentioned this in my former note merely because I [Pg 106] believed that you had come to a similar conclusion, and I like much to be in accord with you. I believe I was mainly deceived by single variations offering such simple illustrations, as when man selects [i.e. isolates][34].

Again, somewhere about the same time, he wrote to Moritz Wagner:—

> Although I saw the effects of isolation in the case of islands and mountain-ranges, and knew of a few instances of rivers, yet the greater number of your facts were quite unknown to me. I now see that, from the want of knowledge, I did not make nearly sufficient use of the views which you advocate[35].

Now it would be easy to show the justice of these self-criticisms by quoting longer passages from earlier editions of the *Origin of Species*; but as this, in view of the above passages, is unnecessary, we may next pass on to another point.

The greatest oversight that Wagner made in his otherwise valuable essays on geographical isolation, was in not perceiving that geographical isolation is only one among a number of other forms of isolation: and, therefore, that although it is perfectly true, as he insisted, that polytypic evolution cannot be effected by natural selection alone, it is very far from true, as he further insisted, that *geographical* isolation is the only means whereby natural selection can be assisted in this matter. Hence it is that, when Darwin said he had not himself "made nearly sufficient use" of geographical isolation as a factor of specific divergence, he quite reasonably added that he could not go so far as Wagner did in regarding such isolation as a condition, *sine qua non*, to divergent evolution in all cases. Nevertheless, he adds the important words, "I almost wish I [Pg 107] could believe in its importance to the same extent with you; for you well show, in a manner which never occurred to me, that it removes many difficulties and objections." These words are important, because they show that Darwin had come to feel the force of the "difficulties and objections" with regard to divergent evolution being possible by means of natural selection alone, and how readily they could be removed by assuming the assistance of isolation. Hence, it is much to be deplored that Wagner presented a single kind of isolation (geographical) as equivalent to the principle of isolation in general. For he thus failed to present the complete—and, therefore, the true—philosophy of the subject to Darwin's mind; and in this, as in certain other respects which I shall notice later on, served rather to confuse than to elucidate the matter as a whole.

To sum up. Although in his later years, as shown by his correspondence, Darwin came to recognize more fully the swamping effects of free intercrossing, and the consequent importance of "separation" for the prevention of these effects, and although in this connexion he likewise came more clearly to distinguish between the "two cases" of monotypic and polytypic evolution, it is evident that he never worked out any of these matters—"thinking it prudent," as he wrote with reference to them in 1878, "now I am growing old, to work at easier subjects[36]." Therefore he never clearly saw, on the one hand, that free intercrossing, far from constituting a "difficulty" to *monotypic* evolution by natural selection, is the very means whereby natural selection is in this [Pg 108] case enabled to operate; or, on the other hand, that, in the case of *polytypic* evolution, the

"difficulty" in question is so absolute as to render such evolution, by natural selection alone, absolutely impossible. Hence, although in one sentence of the *Origin of Species* he mentions three forms of isolation (besides the geographical form) as serving in some cases to assist natural selection in causing "divergence of character" (i. e. polytypic evolution[37]), on account of not perceiving how great and how sharp is the distinction between the two kinds or "cases" of evolution, he never realized that, where "two or more new species" are in course of differentiation, *some* form of isolation other than natural selection must *necessarily* be present, whether or not natural selection be likewise so. The nearest approach which he ever made to perceiving this necessity was in one of his letters to Wagner above quoted, where, after again appealing to the erroneous analogy between monotypic evolution and "unconscious selection," he says:—"But I admit that by this process (i. e. unconscious selection) two or more new species could hardly be formed within the same limited area: some degree of separation, if not indispensable, would be highly advantageous; and here your facts and views will be of great value." But even in this passage the context shows that by "separation" he is thinking exclusively of *geographical* separation, which he rightly enough concludes (as against Wagner) need certainly not be "indispensable." Had he gone a step further, he must have seen that separation, [Pg 109] *in some form or another, is* "indispensable" to polytypic evolution. Instead of taking this further step, however, two years later he wrote to Semper as follows:—

> I went as far as I could, perhaps too far, in agreement with Wagner [i. e. in the last edition of the *Origin of Species*]; since that time I have seen no reason to change my mind; but then I must add that my attention has been absorbed on other subjects[38].

And he seems to have ended by still failing to perceive that the explanation which he gives of "divergence of character" in the *Origin of Species*, can only hold on the unexpressed assumption that free intercrossing is in some way prevented at the commencement, and throughout the development, of each diverging type.

Lastly, we have to consider Darwin's opinion touching the important principle of "Independent Variability." This, it will be remembered, is the principle which ensures that when a portion (not too large) of a species is prevented from interbreeding with the rest of the species, sooner or later a divergence of type will result, owing to the fact that the average qualities of the separated portion at the time of its separation cannot have been exactly the same as the average qualities of the specific type as a whole. Thus the state of Amixia, being a state of what Mr. Gulick calls Independent Generation, will of itself—i.e. even if unassisted by natural selection—induce divergence of type, in a ratio that has been mathematically calculated by Delbœuf.

Darwin wrote thus to Professor Weismann in 1872:— [Pg 110]

> I have now read your essay with very great interest. Your view of the origin of local races through "Amixia" is altogether new to me, and seems to throw an important light on an obscure question[39].

And in the last edition of the *Variation of Animals and Plants* he adds the following paragraph:—

> This view may throw some light on the fact that the domestic animals which formerly inhabited the several districts in Great Britain, and the half-wild cattle lately kept in several British parks, differed slightly from one another; for these animals were prevented from wandering over the whole country and intercrossing, but would have crossed freely within each district or park[40].

Now, although I allow that Darwin never attributed to this principle of Amixia, or Independent Variability, anything like the degree of importance to which, in the opinion of Delbœuf, Gulick, Giard, and myself, it is entitled, the above passage appears to show that, as soon as the "view" was clearly "suggested" to his mind, he was so far from being unfavourably disposed towards it, that he added a paragraph to the last edition of his *Variation* for the express purpose of countenancing it. Nevertheless, later on the matter appears to have entirely escaped his memory; for in 1878 he wrote to Semper, that he did "not see at all more clearly than I did before, from the numerous cases which he [Wagner] has brought forward, how and why it is that a long isolated form should almost always become slightly modified[41]." I think this shows entire forgetfulness of the principle in question, because, if the latter is good for explaining the *initial* [Pg 111] divergence of type as between separated stocks of "domesticated animals," much more must it be competent to explain the *further* divergence of type which is "almost always" observable in the case of "a long isolated form" under nature. The very essence of the principle being that, when divergence of type has once begun, this divergence must *ipso facto* proceed at an ever-accelerating pace, it is manifestly inconsistent to entertain the principle as explaining the first commencement of divergence, and then to ignore it as explaining the further progress of divergence. Hence, I can only conclude that Darwin had forgotten this principle altogether when he wrote his letter to Semper in 1878—owing, no doubt, as he says in the sentence which immediately follows, to his having "not attended much of late years to such questions."

So much, then, for Darwin's opinions. Next in order of time we must consider Moritz Wagner's essays on what he called the "Law of Migration[42]." The merit of these essays was, first, the firm

expression of opinion upon the swamping effects of free intercrossing; and, second, the production of a large body of facts showing the importance of geographical isolation in the prevention of these effects, and in the consequent differentiation of specific types. On the other hand, the defect of these essays was, first, not distinguishing between evolution as monotypic and polytypic; and, second, not perceiving that geographical isolation is only one among a [Pg 112] number of other forms of isolation. From these two radical oversights—which, however, were shared by all other writers of the time, with the partial exception of Darwin himself, as previously shown—there arose the following and most lamentable errors.

Over and over again Moritz Wagner insists, as constituting the fundamental doctrine of his attempted reform of Darwinism, that evolution by natural selection is impossible, unless natural selection be assisted by geographical isolation, in order to prevent the swamping effects of intercrossing[43]. Now, if instead of "evolution" he had said "divergence of type," and if instead of "geographical isolation" he had said "prevention of intercrossing," he would have enunciated the general doctrine which it has been the joint endeavour of Mr. Gulick and myself to set forth. But by not perceiving that "evolution" is of two radically different kinds—polytypic and monotypic—he entirely failed to perceive that, while for one of its kinds the *prevention* of intercrossing is an absolute necessity, for the other of its kinds the *permission* of intercrossing is a necessity no less absolute. And, again, in missing the fact that geographical isolation is but one of the many ways [Pg 113] whereby intercrossing may be prevented, he failed to perceive that, even as regards the case of polytypic evolution, he greatly erred in representing this one form of isolation as being universally a necessary condition to the process. The necessary condition to this process is, indeed, the prevention of intercrossing *by some means or another*; but his unfortunate insistence on geographical separation as the only possible means to this end—especially when coupled with his no less unfortunate disregard of monotypic evolution—caused him to hinder rather than to advance a generalization which he had only grasped in part. And this generalization is, as now so repeatedly stated, that while the form of isolation which we know as natural selection depends for its action upon the intercrossing of all the individuals which it isolates (i. e. selects), when acting alone it can produce only monotypic evolution; but that when it is supplemented by any of the other numerous forms of isolation, it is furnished with the necessary condition to producing polytypic evolution—and this in as many lines of divergent change as there may be cases of this efficient separation.

Nevertheless, while we must lament these shortcomings on the part of Wagner, we ought to remember that he rendered important services in the way of calling attention to the swamping effects of free intercrossing, and, still more, in that of showing the high importance of geographical isolation as a factor of organic evolution. Therefore, although in an elaborate criticism of his views Weismann was easily able to dispose of his generalizations in the imperfect [Pg 114] form that they presented, I do not think it was just in Weismann to remark, "if Wagner had confined himself to the statement that geographical isolation materially assists the process of natural selection, and thus also promotes the origination of new species, he would have met with little or no opposition; but then, of course, in saying this much, he would not have been saying anything new." No doubt, as I have just shown, he *ought* thus (as well as in other and still more important respects not perceived by Prof. Weismann) to have limited his statement; but, had he done so, it does not follow that he would not have been saying anything new. For, in point of fact, in as far as he said what was true, he did say a great deal that was also new. Thus, most of what he said of the *principle of separation* (apogamy) was as new as it was true, although, as we have seen, he said it to very little purpose on account of his identifying this principle as a whole with that of but one of its forms. Again, notwithstanding this great error, or oversight, he certainly showed of the particular form in question—viz. geographical isolation—that it was of considerably *more* importance than had previously been acknowledged. And this was so far a valuable contribution to the general theory of descent.

Prof. Weismann's essay, to which allusion has just been made[44], was, however, in all respects a great advance upon those of Wagner. It was not only more comprehensive in its view of the whole subject of geographical isolation, but likewise much more adequate in its general treatment thereof. Its principal defects, in my judgement, were, first, the inordinately speculative character [Pg 115] of some of its parts, and, second, the restriction of its analysis to but one form of isolation—a defect which it shares with the essays of Wagner, and in quite as high a degree. Furthermore, although this essay had the great merit of enunciating the principle of Amixia, it did so in a very inefficient manner. For not only was this principle adduced with exclusive reference to *geographical* isolation, but even in regard to this one kind of isolation it was presented in a highly inconsistent manner, as I will now endeavour to show.

Weismann was led to perceive the principle in question by the consideration that new specific characters, when they first appear, do not all appear together in the same individuals: they appear one in one individual, another in another, a third in a third, &c.; and it is only in the course of successive generations that they all become blended in the same individuals by free intercrossing. Hence, the eventually emerging constant or specific type is the resultant of all the transitory or varietal types, when these have been fused together by intercrossing. From which Weismann deduces what he considers a general law—namely, that "the constancy of a specific type does not arise suddenly, but gradually; and it is established by the promiscuous crossing of all individuals[45]." From which again it follows, that this constancy must cease so soon as the

condition which maintains it ceases—i. e. so soon as free intercrossing is prevented by the geographical isolation of a portion of the species from its parent stock.

[Pg 116] Now, to begin with, this statement of the principle in question is not a good statement of it. There was no need while stating the doctrine that separation induces differentiation, to found the doctrine on any such highly speculative basis. In point of fact, there is no real evidence that specific types do attain their constancy in the way supposed; nor, for the purposes of the doctrine in question, is it necessary that there should be. For this doctrine does not need to show how the constancy has been *attained*; it only has to show that the constancy is *maintained* by free intercrossing, with the result that when free intercrossing is *by any means* prevented, divergence of character ensues. In short, the correct way of stating the principle is that which has been adopted by Delbœuf and Gulick—namely, the average characters of a separated portion of a species are not likely to be the same as those of the whole species; with the result that divergence of type will be set up in the separated portion by intercrossing within that portion. Or the principle may be presented as I presented it under the designation of "Independent Variability"—namely, "a specific type may be regarded as the average mean of all individual variations, any considerable departure from this average mean being, however, checked by intercrossing," with the result that when intercrossing is prevented between a portion of a species and the rest of the species, "this population is permitted to develop an independent history of its own, shielded from intercrossing with its parent form[46]."

[Pg 117] Not only, however, is Weismann's principle of "Amixia" thus very differently stated from that of my "Independent Variability" (apogamy), or Gulick's "Independent Generation"; but, apparently owing to this difference of statement, the principle itself is not the same. In particular, while Weismann holds with us that when new characters arise in virtue of the mere prevention of intercrossing with parent forms these new characters will be of non-utilitarian kind[47], he appears to think that divergence of character under such circumstances is not likely to go on to a *specific* value. Now, it is of importance to observe why he arrives at this conclusion, which is not only so different from that of Delbœuf, Gulick, and myself, but apparently so inconsistent with his own recognition of the diversifying effect of "Amixia" as regards the formation of *permanent varieties*. For, as we have already seen while considering Darwin's views on this same principle of "Amixia," it is highly inconsistent to recognize its diversifying effect up to the stage of constituting fixed varieties, and then not to recognize that, so much divergence of character having been already secured by the isolation alone, much more must further divergence continue, and continue at an ever accelerating pace—as Delbœuf and Gulick have so well shown. What, then, is the explanation of this apparent inconsistency on Weismann's part? The explanation evidently is that, owing to his erroneous statement of the principle, he misses the real essence of it. For, in the first place, he does not perceive that this essence consists in an initial difference of average characters on the part of the isolated colony as compared with the rest of their species. On the contrary, he loses himself in a maze of speculation about all species [Pg 118] having had what he calls "variation-periods," or eruptions of general variability alternating with periods of repose—both being as unaccountable in respect of their causation as they are hypothetical in respect of their occurrence. From these speculations he concludes, that isolation of a portion of a species will then only lead to divergence of character when the isolation happens to coincide with a "variation-period" on the part of the species as a whole, and that the divergence will cease so soon as the "variation-period" ceases. Again, in the second place as previously remarked, equally with Wagner whom he is criticizing, he fails to perceive that *geographical* isolation is not the only kind of isolation, or the only possible means to the prevention of free intercrossing. And the result of this oversight is, that he thinks amixia can act but comparatively seldom upon sufficiently small populations to become a factor of much importance in the differentiation of species. Lastly, in the third place, owing to his favourite hypothesis that all species pass through a "variation-period," he eventually concludes that the total amount of divergence of type producible by isolation alone (even in a small population) can never be greater than that between the extremes of variation which occur within the whole species at the date of its partition (p. 75). In other words, the possibility of change due to amixia alone is taken to be limited by the range of deviation from the general specific average, as manifested by different individual variations, before the species was divided. Thus the doctrine of amixia fails to recognize the law of Delbœuf, or the *cumulative* nature of divergence of type when [Pg 119] once such divergence begins in a separated section. Therefore, in this all-important—and, indeed, essential—respect, amixia differs entirely from the principle which has been severally stated by Delbœuf, Gulick, and myself.

Upon the whole, then, we must say that although Professor Weismann was the first to recognize the diversifying influence of merely indiscriminate isolation *per se* (apogamy), he did so only in part. He failed to distinguish the true essence of the principle, and by overlaying it with a mass of hypothetical speculation, concealed even more of it than he revealed.

The general theory of Isolation, as independently worked out by Mr. Gulick and myself, has already been so fully explained, that it will here be sufficient merely to enumerate its more distinguishing features. These are, first, drawing the sharpest possible line between evolution as monotypic and polytypic; second, showing that while for the former the peculiar kind of isolation which is presented by natural selection suffices of itself to *transform* a specific type, in order to work for the latter, or to *branch* a specific type, natural selection must necessarily be assisted by

some other kind of isolation; third, that even in the absence of natural selection, other kinds of isolation may be sufficient to effect specific divergence through independent generation alone; fourth, that, nevertheless, natural selection, where present, will always accelerate the process of divergence; fifth, that monotypic evolution by natural selection depends upon the *presence* of intercrossing, quite as much as polytypic evolution (whether with or without natural selection) depends upon the *absence* of it; sixth, that, having regard to the process of evolution throughout all taxonomic divisions of organic nature, we must deem the physiological form of isolation as the most important, with the exception only of natural selection. [Pg 120]

The only difference between Mr. Gulick's essays and my own is, that, on the one hand, he has analyzed much more fully than I have the various forms of isolation; while, on the other hand, I have considered much more fully than he has the particular form of physiological isolation which so frequently obtains between allied *species*. This particular form of physiological isolation I have called "physiological selection," and claim for it so large a share in the differentiation of specific types as to find in it a satisfactory explanation of the contrast between natural species and artificial varieties in respect of cross-infertility.

Mr. Wallace, in his *Darwinism*, has done good service by enabling all other naturalists clearly to perceive how natural selection alone produces monotypic evolution—namely, through the free intercrossing of all individuals which have not been eliminated by the isolating process of natural selection itself. For he very lucidly shows how the law of averages must always ensure that in respect of any given specific character, half the individuals living at the same time and place will present the character above, and half below its mean in the population as a whole. Consequently, if it should ever be of advantage to a species that this character should undergo either increase or decrease of its average size, form, colour, &c., there will always be, in each succeeding generation, a sufficient number of individuals—i. e. half of the whole—which present variations in the required direction, and which will therefore furnish natural selection with abundant material for its action, without the need of any other form of isolation. It is to be regretted, however, that while thus so clearly presenting the fact that free intercrossing is the very means whereby natural selection is enabled to effect monotypic evolution, he fails to perceive that such intercrossing must always and necessarily render it impossible for natural selection to effect polytypic evolution. A little thought might have shown him that the very proof which he gives of the necessity of intercrossing where the *transmutation* of species is concerned, furnishes, measure for measure, as good a proof of the necessity of its absence where the *multiplication* of species is concerned. In justice to him, however, it may be added, that this distinction between evolution as monotypic and polytypic (with the important consequence just mentioned) still continues to be ignored also by other well-known evolutionists of the "ultra-Darwinian" school. Professor Meldola, for example, has more recently said that in his opinion the "difficulty from intercrossing" has been in large part—if not altogether—removed by Mr. Wallace's proof that natural selection alone is capable of effecting [monotypic] evolution; while he regards the distinction between monotypic and polytypic evolution as mere "verbiage[48]." [Pg 121]

It is in relation to my presentment of the impossibility of natural selection alone causing polytypic evolution, that Mr. Wallace has been at the pains to show how the permission of intercrossing (panmixia) is necessary for natural selection in its work of causing monotypic evolution. And not only has he thus failed to perceive that the "difficulty" which intercrossing raises against the view of natural selection being of itself capable of causing polytypic evolution in no way applies to the case of monotypic; but as regards this "difficulty," where it does apply, he says:— [Pg 122]

> Professor G. J. Romanes has adduced it as one of the difficulties which can alone be overcome by his theory of physiological selection[49].

This, however, is a misapprehension. I have by no means represented that the difficulty in question can alone be overcome by this theory. What I have represented is, that it can be overcome by any of the numerous forms of isolation which I named, and of which physiological selection is but one. And although, *where common areas are concerned*, I believe that the physiological form of isolation is the most important form, this is a very different thing from entertaining the supposition which Mr. Wallace here assigns to me.

I may take this opportunity of correcting a somewhat similar misunderstanding which has been more recently published by Professor W. A. Herdman, of Liverpool; and as the case which he gives is one of considerable interest in itself, I will quote his remarks in extenso. In his *Opening Address to the Liverpool Biological Society*, Professor Herdman said:— [Pg 123]

> Some of you will doubtless remember that in last year's address, while discussing Dr. Romanes' theory of physiological selection, I quoted Professor Flemming Jenkin's imaginary case of a white man wrecked upon an island inhabited by negroes, given as an illustration of the supposed swamping effect by free intercrossing of a marked variety with the parent species. I then went on to say in criticism of the result at which Jenkin arrived, viz. that the characteristics of the white man would be stamped out by

intercrossing with the black:—

> "Two influences have, I think, been ignored, viz. atavism, or reversion to ancestral characters, and the tendency of the members of a variety to breed with one another. Keeping to the case described above, I should imagine that the numbers of intelligent young mulattoes produced in the second, third, fourth, and few succeeding generations would to a large extent intermarry, the result of which would be that a more or less white aristocracy would be formed on the island, including the king and all the chief people, the most intelligent men and the bravest warriors. Then atavism might produce every now and then a much whiter individual—a reversal to the characteristics of the ancestral European—who, by being highly thought of in the whitish aristocracy, would have considerable influence on the colour and other characteristics of the next generation. Now such a white aristocracy would be in precisely the same circumstances as a favourable variety competing with its parent species," &c.

You may imagine then my pleasure when, a few months after writing the above, I accidentally found, in a letter[50] written by the celebrated African traveller Dr. David Livingstone to Lord Granville, and dated "Unyanyembe, July 1st, 1872," the following passage:—

> "About five generations ago, a white man came to the highlands of Basañgo, which are in a line east of the watershed. He had six attendants, who all died, and eventually their headman, called Charura, was elected chief by the Basañgo. In the third generation he had sixty able-bodied spearmen as lineal descendants. This implies an equal number of the other sex. They are very light in colour, and easily known, as no one is allowed to wear coral beads such as Charura brought except the royal family. A book he brought was lost only lately. The interest of the case lies in its connexion with Mr. Darwin's celebrated theory on the 'origin of species,' for it shows that an improved variety, as we whites modestly call ourselves, is not so liable to be swamped by numbers as some have thought." [Pg 124]

> Here we have a perfect fulfilment of what I last year, in ignorance of this observation of Livingstone's, predicted as being likely to occur in such a case. We have the whitish aristocracy in a dominant condition, and evidently in a fair way to spread their characteristics over a larger area and give rise to a marked variety, and it had clearly struck Livingstone fourteen years before the theory of physiological selection had been heard of, just as it must strike us now, as an instance telling strongly against the "swamping" argument as used by Flemming Jenkin and Romanes.

Here we have a curious example of one writer supporting the statements of another, while appearing to be under the impression that he is controverting those statements. Both Professor Herdman's imaginary case, and its realization in Livingstone's account, go to show "the tendency of the members of a variety to breed with one another." This is what I have called "psychological selection," and, far from "ignoring" it, I have always laid stress upon it as an obviously important form of isolation or *prevention* of free intercrossing. But it is a form of isolation which can only occur in the higher animals, and, therefore, the whole of Professor Herdman's criticism is merely a restatement of my own views as already published in the paper which he is criticizing. For all that his argument goes to prove is, first, the necessity for *some* form of isolation if the overwhelming effects of intercrossing are to be obviated; and, secondly, the manifest consequence that where the psychological form is unavailable (as in many of the lower animals and in all plants), some other form must be present if divergent evolution is taking place on a common area. [Pg 125]

Seeing that so much misunderstanding has been shown with reference to my views on "the swamping effects of intercrossing," and seeing also that this misunderstanding extends quite as much to Mr. Gulick's views as to my own, I will here supply brief extracts from both our original papers, for the double purpose of showing our complete agreement, and of leaving it to be judged whether we can fairly be held responsible for the misunderstanding in question. After having supplied these quotations, I will conclude this historical sketch by considering what Mr. Wallace has said in reply to the views therein presented. I will transcribe but a single passage from our papers, beginning with my own.

> 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*? How is it that, in the course of evolution, species have not simply become transmuted in linear series instead of ramifying into branches? This question Mr. Darwin seeks to answer "from the simple circumstance that the more diversified the descendants from any one species becomes 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." 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. [Pg 126]

> Now, this argument appears to me unassailable in all save one particular; but this is a most important particular: the argument wholly ignores the fact 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 form in question, that the advantages to be derived from diversification will be most pronounced. 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*, and of their further divergence into *genera*; for in these cases the physiological barrier is known to be already present. But in applying the argument to explain the divergence of individuals into varieties, it seems to me that here, more than anywhere else, Mr. Darwin has strangely 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 that natural selection alone could produce any divergence of specific 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 [Pg 127] 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, 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.

Now for Mr. Gulick, a portion of whose more lengthy discussion of the subject, however, is all that I need quote:—

> Having found that the evolution of the fitted is secured through the prevention of crossing between the better fitted and the less fitted, can we believe that the evolution of a special race, regularly transmitting a special kind of fitness, can be realized without any prevention of crossing with other races that have no power to transmit that special kind of fitness? Can we suppose that any advantage, derived from new powers that prevent severe competition with kindred, can be permanently transmitted through succeeding generations to one small section of the species while there is free crossing equally distributed between all the families of the species? Is it not apparent that the terms of this supposition are inconsistent with the fundamental laws of heredity? Does not inheritance follow the lines of consanguinity; and when consanguinity is widely diffused, can inheritance be closely limited? When there is free crossing between the families of one species, will not any peculiarity that appears in one family either be neutralized by crosses with families possessing the opposite quality, or, being preserved by natural selection, while the opposite quality is gradually excluded, will not the new quality gradually extend to all the branches of the species; so that, in this way or in that, increasing divergence of form will be prevented?
>
> If the advantage of freedom from competition in any given variation depends on the [Pg 128] possession, in some degree, of new adaptations to unappropriated resources, there must be some cause that favours the breeding together of those thus specially endowed, and interferes in some degree with their crossing with other variations, or, failing this, the special advantage will in succeeding generations be lost. As some degree of Independent Generation is necessary for the continuance of the advantage, it is evident that the same condition is necessary for the accumulation through Natural Selection of the powers on which the advantage depends. The advantage of divergence of character cannot be retained by those that fail to retain the divergent character; and divergent character cannot be retained by those that are constantly crossing with other kinds; and the prevention of free crossing between those that are equally successful is in no way secured by Natural Selection.

So much, then, as expressive of Mr. Gulick's opinion upon this subject. To exactly the same effect Professor Lloyd Morgan has recently published his judgement upon it thus:—

> That perfectly free intercrossing, between any or all of the individuals of a given group of animals, is, so long as the characters of the parents are blended in the offspring, fatal to divergence of character, is undeniable. Through the elimination of less favourable variations, the swiftness, strength, and cunning of a race may be gradually

> improved. But no form of elimination can possibly differentiate the group into swift, strong, and cunning varieties, distinct from each other, so long as all three varieties freely interbreed, and the characters of the parents blend in the offspring. Elimination may and does give rise to progress in any given group, *as a group*; it does not and cannot give rise to differentiation and divergence, so long as interbreeding with consequent interblending of characters be freely permitted. Whence it inevitably follows, as a matter of simple logic, that where divergence has occurred, intercrossing and interbreeding must in some way have been lessened or prevented. Thus a new factor is introduced, that of *isolation* or *segregation*. And there is no questioning the [Pg 129]
> fact that it is of great importance. Its importance, indeed, can only be denied by denying the swamping effects of intercrossing, and such denial implies the tacit assumption that interbreeding and interblending are held in check by some form of segregation. The isolation explicitly denied is implicitly assumed[51].

Similarly, and still more recently, Professor Le Conte writes:—

> It is evident, then, as Romanes claims, that natural selection alone tends to *monotypic* evolution. Isolation of some sort seems necessary to *polytypic* evolution. The tree of evolution under the influence of natural selection alone grows palm-like from its terminal bud. Isolation was necessary to the starting of lateral buds, and thus for the profuse ramification which is its most conspicuous character[52].

In order to complete this historical review, it only remains to consider Mr. Wallace's utterances upon the subject.

It is needless to say that he stoutly resists the view of Weismann, Delbœuf, Gulick, and myself, that specific divergence can ever be due—or, as I understand him, even so much as assisted—by this principle of indiscriminate isolation (apogamy). It will be remembered, however, that Mr. Gulick has adduced certain general principles and certain special facts of geographical distribution, in order to prove that apogamy eventually leads to divergence of character, provided that the isolated section of the species does not contain any very large number of individuals. Now, Mr. Wallace, without making any reference to this argument of Mr. Gulick, simply states the reverse—namely, that, as a matter of fact, indiscriminate isolation is not found to be [Pg 130]
associated with divergence of character. For, he says, "there is an entire absence of change, where, if this were a *vera causa*, we should expect to find it[53]." But the only case which he gives is that of Ireland.

This, he says, furnishes "an excellent test case, for we know that it [Ireland] has been separated from Britain since the end of the glacial epoch: ... yet hardly one of its mammals, reptiles, or land molluscs has undergone the slightest change[54]." Here, however, Mr. Wallace shows that he has failed to understand "the views of those who, like Mr. Gulick, believe isolation itself to be a cause of modification of species"; for it belongs to the very essence of these views that the efficiency of indiscriminate isolation as a "*vera causa*" of organic evolution varies inversely with the number of individuals (i. e. the size of the species-section) exposed to its influence. Therefore, far from being "an excellent test case," the case of Ireland is unsatisfactory. If we are in search of excellent test cases, in the sense intended by Mr. Wallace, we ought not to choose a large island, which from the time of its isolation must have contained large bulks of each of the geographically separated species concerned: we ought to choose cases where as small a number as possible of the representatives of each species were in the first instance concerned. And, when we do this, the answer yielded by any really "excellent test case" is unequivocal.

No better test case of this kind has ever been furnished than that of Mr. Gulick's land-shells, [Pg 131]
which Mr. Wallace is specially considering in the part of his book where the sentence above quoted occurs. How, then, does he meet this case? He meets it by assuming that in all the numerous adjacent valleys of a small island there must be as many differences of environment, each of which is competent to induce slight varietal changes on the part of its occupants by way of natural selection, although in no one case can the utility of these slight changes be surmised. Now, against this explanation there are three overwhelming considerations. In the first place, it is purely gratuitous, or offered merely in order to save the hypothesis that there *can* be no other cause of even the most trivial change in species than that which is furnished by natural selection. In the second place, as Mr. Gulick writes to me in a private letter, "if the divergence of Sandwich Island land molluscs is wholly due to exposure to different environments, as Mr. Wallace argues on pages 147-150, then there must be completely occult influences in the environment that vary progressively with each successive mile. This is so violent an assumption that it throws doubt on any theory that requires such support." In the third place, the assumption that the changes in question must have been due to natural selection, is wholly incompatible with the facts of isolation elsewhere—namely, in those cases where (as in that of Ireland) a large section of species, instead of a small section, has been indiscriminately isolated. Mr. Wallace, as we have seen, inadvertently alludes to these "many other cases of isolation" as evidence against apogamy being *per se* a cause of specific change. But although, for the reason above stated, they are [Pg 132]
without relevancy in this respect, they appear to me fatal to the explanation which he gives of specific changes under apogamy where only small sections of species are concerned. For example, can it be rationally maintained that there are more differences of environment between every two of the many contiguous valleys of a small island, such as Mr. Gulick describes, than there are in the incomparably larger area of the whole of Ireland? But, if not, and if natural

selection is able to work such "occult" wonders in each successive mile on the Sandwich Islands, why has it so entirely lost this magic power in the case of Ireland—or in the "many other cases of isolation" to which Mr. Wallace refers? On his theory there is no coherent answer to be given to this question, while on our theory the answer is given in the very terms of the theory itself. The facts are plainly just what the theory requires that they should be; and therefore, if they were not as they are, the theory would be deprived of that confirmation which it now derives from them.

Thus, in truth, though in an opposite way, the case of Ireland is, as Mr. Wallace says, "an excellent test case," when once the theory of apogamy as a "*vera causa*" of specific change is understood; and the effect of applying the test is fully to corroborate this theory, while at the same time it as fully negatives the other. For the consideration whereby Mr. Wallace seeks to explain the inactivity of natural selection in the case of Ireland is not "coherent." What he says is, "That changes have not occurred through natural selection, is perhaps due to the less severe [Pg 133] struggle for existence, owing to the smaller number of competing species[55]." But even with regard to molluscs alone, there is a greatly larger number of species in Ireland than occurs in any one valley of the Sandwich Islands; while if we have regard to all the other classes of animal life, comparison entirely fails.

Much more to the point are certain cases which were adduced long ago by Weismann in his essay previously considered. Nevertheless, although this essay was published as far back as 1872, and, although it expressly deals with the question of divergence of character through the mere prevention of intercrossing (Amixia), Mr. Wallace nowhere alludes to these cases *per contra*, which are so much more weighty than his own "test case" of Ireland. Of such are four species of butterflies, belonging to three genera[56], which are identical in the polar regions and in the Alps, notwithstanding that the sparse Alpine populations have been presumably separated from their parent stocks since the glacial period; or of certain species of fresh water crustaceans (*Apus*), the representatives of which are compelled habitually to form small isolated colonies in widely separated ponds, and nevertheless exhibit no divergence of character, although apogamy has probably lasted for centuries. These cases are unquestionably of a very cogent nature, and appear of themselves to prove that apogamy alone is not invariably capable of inducing [Pg 134] divergence—at any rate, so rapidly as we might expect. There appears, however, to be another factor, the presence or absence of which makes a great difference. This as stated in the text, is the degree in which a specific type is stable or unstable—liable or not liable to vary. Thus, for example, the Goose is what Darwin calls an "inflexible" type as compared with most other domesticated birds. Therefore, if a lot of geese were to be indiscriminately isolated from the rest of their species, the probability is that in a given time their descendants would not have diverged from the parent type to such an extent as would a similar lot of ducks under similar circumstances: the more stable specific type would require a longer time to change under the influence of apogamy alone. Now, the butterflies and crustaceans quoted by Weismann may be of a highly stable type, presenting but a small range of individual variability; and, if so, they would naturally require a long time to exhibit any change of type under the influence of apogamy alone. But, be this as it may, Weismann himself adduces these cases merely for the sake of showing that there are cases which seem to tell against the general principle of modification as due to apogamy alone—i.e. the general principle which, under the name amixia, he is engaged in defending. And the conclusion at which he himself arrives is, that while it would be wrong to affirm that apogamy *must* in all cases produce divergence, we are amply justified in affirming that in many cases it *may* have done so; while there is good evidence to prove that in not a few cases it *has* done so, and therefore should be accepted as one of the factors of organic [Pg 135] evolution[57].

My view from the very first has been that variations in the way of cross-infertility are of frequent occurrence (how, indeed, can they be otherwise, looking to the complex conditions that have to be satisfied in every case of full fertility?); and, therefore, however many of such variations are destined to die out, whenever one arises, "under suitable conditions," "it must inevitably tend to be preserved as a new natural variety, or incipient species." Among the higher animals—which are "comparatively few in number"—I think it probable that some slight change of form, colour, habit, &c., must be usually needed either to "superinduce," or, which is quite a different thing, to *coincide* with the physiological change But in the case of plants and the lower invertebrata. I see no reason for any frequent concomitance of this kind; and therefore believe the physiological [Pg 136] change to be, "as a general rule," the primordial change. At the same time, I have always been careful to insist that this opinion had nothing to do with "the essence of physiological selection"; seeing that "it was of no consequence" to the theory in what proportional number of cases the cross-sterility had begun *per se*, had been superinduced by morphological changes, or only enabled to survive by happening to coincide with any other form of homogamy. In short, "the essence of physiological selection" consists in *all* cases of the diversifying *effect* of cross-infertility, whensoever and howsoever it may happen in particular cases to have been *caused*.

Thus I emphatically reaffirm that "from the first I have always maintained that it makes no essential difference to the theory *in what proportional number of cases* they [the physiological variations] have arisen 'alone in an otherwise undifferentiated species'"; therefore, "even if I am wrong in supposing that physiological selection can *ever* act alone, the *principle* of physiological selection, as I have stated it, is not thereby affected. And this principle is, as Mr. Wallace has re-stated it, 'that some amount of infertility characterizes the distinct varieties which are in process of differentiation into species'—infertility whose absence, 'to obviate the effects of intercrossing, may be one of the *usual* causes of their failure to become developed into distinct species.'"

These last sentences are quoted from the correspondence in *Nature*[58], and to them Mr. Wallace replied by saying, "if this is not an absolute change of front, words have no meaning"; that "if this [Pg 137] is 'the whole essence of physiological selection,' then physiological selection is but a re-statement and amplification of Darwin's views"; that such a "change of front" is incompatible, not only with my term "physiological selection," but also with my having "acknowledged that Mr. Catchpool had 'very clearly put forward the theory of physiological selection'"; and much more to the same effect.

Now, to begin with, it is due to Mr. Catchpool to state that his only publication upon this subject is much too brief to justify Mr. Wallace's, inference, that he supposes variations in the way of cross-infertility always to arise "alone in an otherwise undifferentiated species." What Mr. Catchpool's opinion on this point may be, I have no knowledge; but, whatever it is, he was unquestionably the first writer who "clearly stated the leading principles" of physiological selection, and this fact I am very glad to have "acknowledged." In my correspondence with Mr. Wallace, however, I not only named Mr. Catchpool: I also named—and much more prominently—Mr. Gulick. For even if I were to grant (which I am far indeed from doing) that there was any want of clearness in my own paper touching the point in question, I have now repeatedly shown that it is simply impossible for any reader of Mr. Gulick's papers to misunderstand *his* views with regard to it. Accordingly, I replied to Mr. Wallace in *Nature* by saying:—

> Not only have I thus from the first fully recognized the sundry other causes of specific change with which the physiological variations may be associated; but Mr. Gulick has gone into this side of our common theory much more fully, and elaborately calculated [Pg 138] out the high ratio in which the differentiating agency of any of these other causes must be increased when assisted by—i. e. associated with—even a moderate degree of the selective fertility, and vice versa. Therefore, it is simply impossible for Mr. Wallace to show that "our theory" differs from his in this respect. Yet it is the only respect in which his reply alleges any difference. (Vol. xliii. p. 127.)

I think it is to be regretted that, in his answer to this, Mr. Wallace alludes only to Mr. Catchpool, and entirely ignores Mr. Gulick—whose elaborate calculations above alluded to were communicated to the Linnaean Society by Mr. Wallace himself in 1887.

The time has now come to prove, by means of quotations, that I have from the first represented the "principle," or "essence," of physiological selection to consist in selective fertility furnishing a needful condition to specific differentiation, in at least a large proportional number of allied species which afterwards present the reciprocal character of cross-sterility; that I have never represented variations in the way of this selective fertility as necessarily constituting the initial variations, or as always arising "alone, in an otherwise undifferentiated species"; and that, although I have uniformly given it as my opinion that these variations do *in some cases* thus arise (especially among plants and lower invertebrata), I have as uniformly stated "that it makes no difference to the theory in what proportional number of cases they have done so"—or even if, as Mr. Wallace supposes, they have never done so in any case at all[59]. These statements (all of [Pg 139] which are contradictory of the only points of difference alleged) have already been published in my article in the *Monist* of October, 1890. And although Mr. Wallace, in his reply to that article, ignores my references to the "original paper," it is scarcely necessary to quote the actual words of the paper itself, since the reader who is further interested in this controversy can readily refer to it in the *Journal of the Linnaean Society* (vol. xix. pp. 337-411).

Having arrived at these results with regard to the theory of Isolation in general and of Physiological Isolation in particular, I arrive also at the end of this work. And if, while dealing with the post-Darwinian period, I have imparted to any general reader the impression that there is still a great diversity of expert opinion; I must ask him to note that points with reference to which disagreement still exists are but very subordinate to those with regard to which complete agreement now prevails. The noise of wrangling disputations which has so filled the camp of evolutionists since the death of their captain, is apt to hide from the outside world the solid unanimity that prevails with regard to all the larger and more fundamental questions, which were similarly the subjects of warfare in the past generation. Indeed, if we take a fair and general view [Pg 140] of the whole history of Darwinism, what must strike us as the really significant fact is the astonishing unanimity which has been so rapidly attained with regard to matters of such immeasurable importance. It is now but little more than thirty years since the publication of the *Origin of Species*; and in that period not only have all naturalists unequivocally embraced the doctrine of descent considered as a fact; but, in one degree or another, they have all as unequivocally embraced the theory of natural selection considered as a method. The only points with regard to which any difference of opinion still exist, have reference to the precise causation of that mighty stream of events which, under the name of organic evolution, we have now all learnt to accept as scientifically demonstrated. But it belongs to the very nature of scientific demonstration that, where matters of great intricacy as well as of high generality are concerned, the process of demonstration must be gradual, even if it be not always slow. It is only by the labours of many minds working in many directions that, in such cases, truth admits of being eventually displayed. Line upon line, precept upon precept, here a little and there a little—such is the course of a scientific revelation; and the larger the subject-matter, the more subtle and the more complex the causes, the greater must be the room for individual differences in our reading of the book of Nature. Now, if all this be true, must we not feel that in the matter of organic evolution the measure of agreement which has been attained is out of all proportion to the differences which still remain—differences which, although of importance in themselves, are

insignificant when compared with those which once divided the opinions of not a few still living men? And if we are bound to feel this, are we not bound further to feel that the very intensity of our disputations over these residual matters of comparative detail, is really the best earnest that can be given of the determination of our quest—determination which, like that of our fathers, cannot fail to be speedily rewarded by the discovery of truth? [Pg 141]

Nevertheless, so long as this noise of conflict is in the Senate, we cannot wonder if the people are perplexed. Therefore, in conclusion, I may ask it to be remembered exactly what are the questions—and the only questions—which still divide the parties.

Having unanimously agreed that organic evolution is a fact and that natural selection is a cause, or a factor in the process, the primary question in debate is whether natural selection is the only cause, or whether it has been assisted by the co-operation of other causes. The school of Weismann maintain that it is the only cause; and therefore deem it worse than useless to search for further causes. With this doctrine Wallace in effect agrees, excepting as regards the particular case of the human mind. The school of Darwin, on the other hand—to which I myself claim to belong—believe that natural selection has been to a considerable extent supplemented by other factors; and, therefore, although we further believe that it has been the "main" factor, we agree with Darwin himself in strongly reprobating all attempts to bar *a priori* the progress of scientific investigation touching what, if any, these other factors may be. Lastly, there are several more or less struggling schools, chiefly composed of individual members who agree with each other only to the extent of holding that the causal agency of natural selection is not so great as Darwin supposed. The Duke of Argyll, Mr. Mivart and Mr. Geddes may be named in this connexion; together with the self-styled neo-Lamarckians, who seek to magnify the Lamarckian principles at the expense of the distinctively Darwinian. [Pg 142]

This primary difference of opinion leads deductively to certain secondary differences. For if a man starts with the premiss that natural selection must necessarily be the "exclusive" cause of organic evolution, he is likely to draw conclusions which another man would not draw who starts with the premiss that natural selection is but the "main" cause. Of these subordinate differences the most important are those which relate to the possible transmission of acquired characters, to the necessary (or only general) utility of specific characters, and to the problem touching the inter-sterility of allied species. But we may well hope that before another ten years shall have passed, even these still outstanding questions will have been finally settled; and thus that within the limits of an ordinary lifetime the theory of organic evolution will have been founded and completed in all its parts, to stand for ever in the world of men as at once the greatest achievement in the history of science, and the most splendid monument of the nineteenth century.

In the later chapters of the foregoing treatise I have sought to indicate certain matters of general principle, which many years of study specially devoted to this great movement of contemporary thought have led me to regard as almost certainly sound in themselves, and no less certainly requisite as complements of the Darwinian theory. I will now conclude by briefly summarizing these matters of general principle in the form of twelve sequent propositions. And, in doing so, I may ask it to be noticed that the system which these propositions serve to express may now claim, at the least, to be a strictly logical system. For the fact that, not merely in its main outlines, but likewise in its details, it has been independently constructed by Mr. Gulick, proves at any rate this much; seeing that, where matters of such intricacy are concerned, nothing but accurate reasoning from a common foundation of *data* could possibly have yielded so exact an agreement. The only difference between us is, that Mr. Gulick has gone into much further detail than I have ever attempted in the way of classifying the many and varied forms of isolation; while I have laid more special stress upon the physiological form, and found in it what appears to me a satisfactory solution of "the greatest of all the difficulties in the way of accepting the theory of natural selection as a complete explanation of the origin of species"—namely, "the remarkable difference between varieties and species when crossed." [Pg 143]

GENERAL CONCLUSIONS. [Pg 144]

1. Natural Selection is primarily a theory of the cumulative development of adaptations wherever these occur; and therefore is only incidentally, or likewise, a theory of the origin of species in cases where allied species differ from one another in respect of peculiar characters, which are also adaptive characters.

2. Hence, it does not follow from the theory of natural selection that all species—much less all specific characters—must necessarily have owed their origin to natural selection; since it cannot be proved deductively from the theory that no "means of modification" other than natural selection is competent to produce such slight degrees of modification as go to constitute diagnostic distinctions between closely allied species; while, on the other hand, there is an overwhelming mass of evidence to prove the origin of "a large proportional number of specific characters" by causes of modification other than natural selection. [Pg 145]

3. Therefore, and upon the whole, as Darwin so emphatically held, "Natural selection has been the main, but not the exclusive means of modification."

4. Even if it were true that all species and all specific characters must necessarily owe their origin to natural selection, it would still remain illogical to define the theory of natural selection as indifferently a theory of species or a theory of adaptations; for, even upon this erroneous supposition, specific characters and adaptive characters would remain very far indeed from being conterminous—most of the more important adaptations which occur in organic nature being the common property of many species.

5. In no case can natural selection have been the cause of mutual infertility between allied, or any other, species—*i.e.* of the most general of all "specific characters."

6. Without Isolation, or the prevention of free intercrossing, organic evolution is in no case possible. Therefore, it is isolation that *has* been "the exclusive means of modification," or, more correctly, the universal condition to it. Therefore, also, Heredity and Variability being given, the whole theory of organic evolution becomes a theory of the causes and conditions which lead to Isolation. [Pg 146]

7. Isolation may be either discriminate or indiscriminate. When discriminate, it has reference to resemblances between individuals constituting the isolated colony or group; when indiscriminate, it has no such reference. In the former case there arises Homogamy, and in the latter case there arises Apogamy.

8. Except where very large populations are concerned, indiscriminate isolation always tends to become increasingly discriminate; and, in the measure that it does so, apogamy passes into homogamy, by virtue of Independent Variability.

9. Natural Selection is one among many other forms of discriminate isolation, and presents in this relation the following peculiarities:—(*a*) The isolation is with reference to superiority of fitness; (*b*) is effected by death of the excluded individuals; and (*c*) unless assisted by some other form of isolation, can only effect monotypic as distinguished from polytypic evolution.

10. It is a general law of organic evolution that the number of possible directions in which divergence may occur can never be more than equal to the number of cases of efficient isolation; but, excepting natural selection, any one form of isolation need not necessarily require the co-operation of another form in order to create an additional case of isolation, or to cause polytypic as distinguished from monotypic evolution. [Pg 147]

11. Where common areas and polytypic evolution are concerned, the most general and most efficient form of isolation has been the physiological, and this whether the mutual infertility has been the antecedent or the consequent of morphological changes on the part of the organisms concerned, and whether or not these changes are of an adaptive character.

12. This form of isolation—which, in regard to incipient species, I have called Physiological Selection—may act either alone or in conjunction with other forms of isolation on common areas: in the former case its agency is of most importance among plants and the lower classes of animals; in the latter case its importance consists in its greatly intensifying the segregative power of whatever other form of isolation it may be with which it is associated.

APPENDICES [Pg 149]

APPENDIX A. [Pg 151]
Mr. Gulick's Criticism of Mr. Wallace's Views on Physiological Selection.

I have received from Mr. Gulick the results of his consideration of Mr. Wallace's criticism. As these results closely resemble those which I have myself reached, and as they were independently worked out on the other side of the globe, I deem it desirable to publish them here for the sake of comparison.

In his covering letter Mr. Gulick writes:—

> Mr. Wallace has most certainly adopted the fundamental principles of our theory, and in an arbitrary way attempted to claim the results produced by these principles as the effects of natural selection. He takes our principles, which in the previous chapter he has combated; but he makes such disjointed use of them that I am not willing to recognize his statement as an intelligible exposition of our theory.... I have endeavoured to indicate at what points Mr. Wallace has deserted his own principles, and at what points he has failed to make the best use of ours. To bring out these points distinctly has been no easy task; but if you regard this paper on *The Preservation and Accumulation of Cross-infertility* as giving any help in elucidating the true principles, and in showing Mr. Wallace's position in regard to them, I shall be satisfied. Please make any use of it that may seem desirable, and then forward it to Professor Dana.

The following is a general summary of Mr. Gulick's results:— [Pg 152]

> Mr. Wallace's criticism of the theory of Physiological Selection is unsatisfactory; (l) because he has accepted the fundamental principle of that theory on pages 173-9, in that he maintains that without the cross-infertility the incipient species there considered would be swamped; (2) because he assumes that physiological selection pertains simply to the infertility of first crosses, and has nothing to do with the infertility of mongrels and hybrids; (3) because he assumes that infertility between first crosses is of rare occurrence between species of the same genus, ignoring the fact that in many species of plants the pollen of the species is pre-potent on the stigma of the same species when it has to compete with the pollen of other species of the same genus; (4) because he not only ignores Mr. Romanes' statement that cross-infertility often affects "a whole race or strain," but he gratuitously assumes that the theory of Physiological Selection excludes this "racial incompatibility" (which Mr. Romanes maintains is the more probable form), and bases his computation on the assumption that the cross-infertility is not associated with any other form of segregation; (5) because he claims to show that "all infertility not correlated with some *useful* variation has a constant tendency to effect its own elimination," while his computation only shows that, if the cross-infertility is not associated with some form of *positive* segregation, it will disappear[60]; and (6) because he does not observe that the positive segregation may be secured by the very form of the physiological incompatibility.... Without here entering into any computation, it is evident that, e.g. the prepotency of pollen of each kind with its own kind, if only very slight, will prevent cross-fertilization as effectually as a moderate degree of instinctive preference in the case of an animal.

The paper likewise indicates a point which, in studying Mr. Wallace's theory, I have missed. It [Pg 153] will be remembered that the only apparent difference between his theory and mine has been shown to consist in this—that while I was satisfied to state, in a general way, that natural selection is probably able to increase a selective fertility which has already been begun by other causes, Mr. Wallace has sought to exhibit more in detail the precise conditions under which it can do so. Now, Mr. Gulick shows that the particular conditions which Mr. Wallace describes, even if they do serve to promote an increase of cross-infertility, are conditions which preclude the possibility of natural selection coming into play at all. So that if, under these particular conditions, a further increase of cross-infertility does take place, it does not take place in virtue of natural selection. To me it appears that this criticism is sound; and, if so, it disposes of even the one very subordinate addition to our theory which Mr. Wallace "claims" as the most "distinctive" part of his.

The following is the criticism in question:—

> On pages 173-186 Mr. Wallace maintains that "Natural selection is, in some probable cases at all events, able to accumulate variations in infertility between incipient species" (p. 174); but his reasoning does not seem to me conclusive. Even if we grant that the increase of this character [cross-infertility] occurs by the steps which he describes, *it is not a process of accumulation by natural selection*. In order to be a means of cumulative modification of varieties, races, or species, selection, whether artificial or adaptational [i.e. natural], must preserve certain forms of an intergenerating stock, to the exclusion of other forms of the same stock. Progressive change in the size of the occupants of a poultry-yard may be secured by raising only bantams the first, only common fowls the second, and only Shanghai fowls the third year; but this is not the form of selection that has produced the different races of fowls. So in nature, rats may drive out and supplant mice; but this kind of selection modifies [Pg 154] neither rats nor mice. On the other hand, if certain variations of mice prevail over others, through their superior success in escaping their pursuers, then modification begins. Now, turning to page 175, we find that, in the illustrative case introduced by Mr. Wallace, the commencement of infertility between the incipient species is in the relations to each other of two portions of a species that are locally segregated from the rest of the species, and partially segregated from each other by different modes of life. These two local varieties, being by the terms of his supposition better adapted to the environment than the freely interbreeding forms in other parts of the general area, increase till they supplant these original forms. Then, in some limited portion of the general area, there arise two still more divergent forms, with greater mutual infertility, and with increased adaptation to the environment, enabling them to prevail throughout the whole area. The process here described, if it takes place, is not modification by natural selection.

On the other hand, it *is* modification by physiological selection. For, among the several other forms of isolation which are called into requisition, the physiological (i.e. ever accumulating cross-infertility) is supposed to play an important part. That the modification is not modification by natural selection may perhaps be rendered more apparent by observing, that in as far as *any* other mode of isolation is involved or supposed, so far is the *possible* agency of natural selection eliminated *as between the two or more otherwise isolated sections of a species*; and yet it is modes of isolation other than that furnished by natural selection (i.e. perishing of the less fit), that Mr. Wallace here supposes to have been concerned—including, as I have before shown, the physiological form, to which, indeed, he really assigns most importance of all. Or, as Mr. Gulick

states the matter in his independent criticism:—

> In the supposed case pictured by Mr. Wallace, the principle by which the two segregating forms are kept from crossing, and so are eventually preserved as permanently distinct forms, is no other than that which Mr. Romanes and myself have discussed under the terms Physiological Selection and Segregate Fecundity. Not only is Mr. Wallace's exposition of the divergence and the continuance of the same in accord with these principles which he has elsewhere rejected, but his whole exposition is at variance with his own principle, which, in the previous chapter, he vigorously maintains in opposition to my statement that many varieties and species of Sandwich Island land molluscs have arisen, while exposed to the same environment, in the isolated groves of the successive valleys of the same mountain range. If he adhered to his own theory, "the greater infertility between the two forms in one portion of the area" would be attributed to a difference between the *environment* presented in that portion and that presented in the other portions; and the difficulty would be to consistently show how this greater infertility could continue unabated when the varieties thus characterized spread beyond the environment on which the character depends. But, without power to continue, the process which he describes would not take place. Therefore, in order to solve the problem of the *origin* and *increase* of infertility between species, he tacitly gives up his own theory, and adopts not only the theory of Physiological Selection but that of Intensive Segregation[61] through Isolation, though he still insists on calling the process natural selection; for on page 183 he says, "No form of infertility or sterility between the individuals of a species can be increased by natural selection unless correlated with some useful variation, while all infertility not so correlated has a constant tendency to effect its own elimination." Even this claim he seems to unwittingly abandon when on page 184 he says: "The moment it [a species] becomes separated either by geographical or selective isolation, or by diversity of station or of habits, then, while each portion must be kept fertile *inter se*, there is nothing to prevent infertility arising between the two separated portions." [Pg 155]

The criticism proceeds to show yet further inconsistencies and self-contradictions in Mr. Wallace's treatment of this subject; but it now seems needless to continue. Nor, indeed, should I have quoted this much but for the sake of so fully justifying my own criticism by showing the endorsement which it has received from a completely independent examination. [Pg 156]

APPENDIX B. [Pg 157]

An Examination by Mr. Fletcher Moulton of Mr. Wallace's Calculation touching the Possibility Of Physiological Selection ever acting alone.

We have seen that the only important point of difference between Mr. Wallace's more recent views and my own on the problem of inter-specific sterility, has reference to the question whether variations in the way of cross-infertility can *ever* arise and act "alone, in an otherwise undifferentiated species," or whether they can *never* so arise and act. It is Mr. Wallace's opinion that, even if they ever do arise alone, at all events they can never act in differentiating a specific type, seeing that the chances against their suitable mating must be so great: only if they be from the first associated with some other form of homogamy, which will have the effect of determining their suitable mating, does he think that they can act in the way supposed by our theory of "selective fertility"[62]. On the other hand, as previously and frequently stated, I have so strong a belief in the segregating power of physiological selection, or selective fertility, that I do not think it is necessary for this principle to be *always* associated with some other form of homogamy. From the first, indeed, I have laid great stress (as, also, has Mr. Gulick) on the re-enforcing influence which association with any other form of homogamy must exercise upon the physiological form, and vice versa; but I have also said that, in my opinion, the physiological form may in many cases be able to act entirely alone, or without assistance derived from any other source. The question here is, as we have already so fully seen, a question of but secondary importance; since, whether or not the physiological form of homogamy ever acts alone, even Mr. Wallace now allows, or rather argues, that it acts in combination—and this so habitually, as well as with so much effect, that it constitutes a usual condition to the origination of species. Nevertheless, although the only relevancy of his numerical computation of chances—whereby he thinks that he overturns my theory *in toto*—is such relevancy as it bears to this question of secondary importance, I have thought it desirable to refer the question, together with Mr. Wallace's views upon it, to the consideration of a trained mathematician. [Pg 158]

As this "subordinate question" depends entirely on numerical computations involving the doctrine of chances, I should first of all like to remark, that in reference to biological problems of the kind now before us, I do not myself attach much importance to a merely mathematical analysis. The conditions which such problems involve are so varied and complex, that it is impossible to be sure about the validity of the *data* upon which a mathematical analysis is founded. Nevertheless, for the sake of meeting these criticisms upon their own ground, I will endeavour to show that, [Pg 159]

even as mathematical calculations, they are quite untrustworthy. And, in order to do this effectually, I will quote the results of a much more competent, as well as a much more thorough, inquiry. I applied to Mr. Moulton for this purpose, not only because he is one of the ablest mathematicians of my acquaintance; but also because his interest in biology, and his knowledge of Darwinian literature, render him well fitted to appreciate exactly, and in all their bearings, the questions which were submitted to his consideration. I need only add that his examination was completely independent, and in no way influenced by me. Having previously read my paper on *Physiological Selection*, Mr. Gulick's paper on *Divergent Evolution*, and Mr. Wallace's book on *Darwinism*, he was in possession of all the materials; and I merely requested the favour of his opinion upon the whole case from a mathematical point of view. The following is his reply; and I give it *in extenso*, because it serves to place in another light some of the general considerations which it has already been my endeavour to present[63].

After some introductory remarks on Mr. Wallace's "adoption of the theory of physiological selection pure and simple," and "the pure caricature of it which he puts forward as" mine, the letter proceeds thus:—

> The reason why it is so easy to attack your theory is that it is so easy to confuse the survival of an *individual* with the survival of a *peculiarity* of *type*. No one has ever said [Pg 160] that an *individual* is *assisted* by the possession of selective fertility: that is a matter which cannot affect his chance of *life*. Nor has any one said that the possession of selective fertility in an *individual* will *of itself* increase the chance of his having *progeny* that will survive, and in turn become the progenitors of others that will survive. Taken by itself, the fact that an *individual* is capable of fertility with some only of the opposite sex lessens the chance of his having progeny. Whether or not he is more or less favourably situated than his *confreres* for the battle of life must be decided by the *total sum* of his peculiarities; and the question whether or not this selective fertility will be a hindrance must be decided by considerations depending on the other peculiarities associated with it.
>
> But when we come to consider the survival or permanence of a *type* or *peculiarity*, the case is quite different. It then becomes not only a favourable circumstance, but, in my opinion, almost a necessary condition, that the peculiarity should be associated with selective fertility[64].
>
> Take the case of the Jews. I don't think that intermarriage with other nations would lessen their fertility, or diminish the number of their progeny; nor is there any reason to think that this progeny would be unequal to the struggle for existence. But no one doubts that the abandonment of their voluntary isolation (which operates so far as this is concerned as a selective fertility), would lead to the disappearance of the familiar Jewish type. All the world would get some of it; but as a whole it would be "swamped."
>
> Now although no doubt Wallace would admit all this, he fails to give it the weight it ought to have. In discussing the question of its operation he considers too exclusively the case of the individual.
>
> Of course, a type can only be perpetuated through the medium of individuals, and all [Pg 161] that his argument amounts to is, that selective fertility would be so fatal to individuals that *no* type which presents it could be formed or perpetuated—a conclusion which is not only absurd in itself, but contradicted by his own subsequent adoption of your theory. Besides, apart from calculations (with which I will deal when I write next), such reasoning brings its own refutation. Selective fertility is not in the same category as some of the other influences to which an important share has been ascribed in the formation of the existing types. *It exists as a recognized phenomenon.* Hence all these numerical proofs that it would lead to extinction, because it is so disadvantageous to the possessor, prove too much. They would show that the degree of selective fertility which so frequently characterizes species is a most onerous gift; and that, were it not present, there would be a vastly increased chance of fertility, which would render the races fitter and lead to their increased survival. Why then has it not been got rid of?
>
> The two answers which no doubt would be given seem to me to support rather than to make against your theory. In the first place, Wallace might say that this infertility is an advantage because it keeps pure a type which is specially fitted to its surroundings, as shown by its continued existence. But if this be so, and it is necessary to protect the *developed* type, how much more necessary to protect the *incipient* type! In the second place, he might say that this selective fertility is not so disadvantageous when the species has been formed, because the individual can choose his mate from his like; whereas, when it is beginning to be formed, he must mate blindly, or without what you call "psychological selection." But this seems to me to be wholly inapplicable to at least half the animal, and to all the vegetable kingdom. Moreover, with regard to the other half of the animal kingdom, it merely raises the question,—How soon will such an incipient type recognize itself? Seeing it is probable that many families [broods] will belong to the same [incipient] type, I should not be surprised if it were found that this sexual recognition and preference sets in very early.
>
> But this leads me to the question of your letter. I understand you to want me to examine and criticize the attempted numerical arguments against or for your theory. [Pg 162]

Now it seems to me that it will be best to take, in the first instance, the vegetable kingdom, and with regard to it I cannot see how there can be any numerical argument against the theory. For we often have species side by side with others nearly allied, but much more numerous. The condition of these is precisely analogous to that of your incipient species. They are exposed to fertilization from, say, ten times as numerous individuals of the allied species. They reject this in favour of that from the relatively few individuals of their own. Yet the two species are in competition. I could go through the numerical arguments of your assailant word for word, applying them to such a case as this, and they would triumphantly show that the specific fertility of the rarer kind would lead to its certain extinction. Yet we know that this is not so.

Indeed, the too triumphant character of the logic used against you seems to me to be capable of being turned to your use. If cross-infertility is so intensely disadvantageous to the individuals presenting it, it cannot have been *that* which made these individuals and their progeny survive. It is therefore a burden which they have carried. But we find that it is more or less present in all the closely allied types that occur on common areas: therefore it must be a necessary feature in the formation of such types; for it cannot be an accident that it is present in so many. In other words, it must be the price which the individual and his progeny pay for their formation into a type. And this is your theory pure and simple.

The more I consider the matter, the more I feel that it is impossible to decide as to the sufficiency of selective fertility to explain the formation of species, if we consider merely the effect it would have on the number of individuals, as contrasted with what it would be if no such peculiarity had developed itself. Indeed, I may say that on pondering over the matter I have come to the conclusion, that mere fertility is probably a comparatively unimportant factor in the preservation of the species, after a certain sufficient degree of fertility is attained. I do not wish to be misunderstood. To a certain point fertility is not only advantageous but necessary, in order to secure survival of the [Pg 163] type; but I feel that little reliance can be placed on calculations based on the numerical co-efficient of fertility (i. e. the ratio of the number of offspring to the number of parents) in determining the relative chance of type-survival.

Take, for instance, the oak tree. It produces thousands of acorns, almost the whole of which die without producing any progeny. Have we any reason to believe that if the number of acorns borne by oak trees were diminished, even so much as to one-tenth, the race of oaks would perish? It may of course be said that, if all other things are equal, the probabilities of survival must be increased by increased fertility of this kind; but I feel convinced that when numerical fertility has attained to a high point in circumstances in which actual increase of the race cannot take place to any substantial extent, the numerical value of this fertility sinks down into a factor of the second or third order of importance—that is to say, into the position of a factor whose effects are only to be considered when we have duly allowed for the full effects of all the main factors. Until we have done that, we gain little or nothing in the way of accuracy of conclusion by taking into consideration the minor factors. It may be very well to neglect the effect of the attraction of Jupiter in our early researches on the motion of the Moon; and our doing so will not prevent the results being approximate and having considerable value, because we are retaining the two main factors that establish the motion, viz. the effects of the Earth and the Sun. But if we exclude the effect of one of these main factors, our results would be worthless; and it would not be rendered substantially less so by the fact that we had taken Jupiter into account in arriving at them.

You must not imagine, however, that I think it wholly profitless to see whether there would be any substantial effect on numerical fertility were *selective* fertility to manifest itself. But if we want to derive any assistance from calculation, it must be by applying it with a good deal more precision and definiteness than anything that Wallace shows. And, in the first place, it is useless to confuse the vegetable and animal kingdoms. In the former you have union unaffected by choice; in the latter, so far at all events as the [Pg 164] higher animals are concerned, you have "psychological selection." In order to give you a specimen of what can safely be done by calculation if you take a problem of sufficient definiteness, I have chosen the case of a flowering plant in which a certain proportion of the race have developed the peculiarity of being sterile with the remainder, while retaining the normal fertility of the race in unions among themselves. In order to give the greatest advantage to your critics, I have assumed that such flowers as possess the peculiarity are not self-fertilizable; for it is clear that if we suppose that they are self-fertilizable, the fertility need be very slightly affected.

As I have excluded self-fertilization, it is necessary, if we are to get any trustworthy results, that one should consider the mode in which fertilization will be produced. I have taken the case of fertilization by insects, and have assumed that each flower is visited a certain number of times by insects during the period when fertilization is possible; and, further, that the insects which visit it have on the average visited a certain number of flowers of the same species before they came there. Of course nothing but observation can fix these latter numbers; but I should not be surprised at finding that they are of considerable magnitude[65]. In order to make the results a little [Pg 165]

more intelligible, I have grouped them under the numbers which represent the average number of flowers that an insect visits in a journey. This is a little more than twice as great as the number which represents the number of flowers he has on the average visited before coming to the individual whose fertility we are considering.

I send you the formula and the calculation on which it is based in an Appendix; but as I know you have a holy horror of algebraical formulae, I give you here a few numerical results.

The cases I have worked out are those in which the number of insects visiting each flower is 5, or 10, or 15; and I have also taken 5, 10, and 15, to represent the number of flowers which an insect visits each journey. This makes nine cases in all; and I have applied these to two instances—viz. one in which one-fifth of the whole race have developed cross-infertility, and the other in which one-tenth only have done so. Taking first the instance where one-fifth have developed the peculiarity, I find that if on the average five insects visit a flower, and each insect on the average visits five flowers on a journey, the fertility is diminished by about one-tenth. If, however, the average number of flowers the insect visits is ten, the reduction of fertility is less than one per cent. And it becomes inappreciable if the average number is fifteen. If on the average ten insects visit each flower, then, if each insect visits on the average five flowers on a journey, the reduction of fertility is a little over one per cent.; but if it visits ten or fifteen the reduction is inappreciable. If fifteen insects visit the flower on an average, then, if these insects on the average visit five or more flowers on a journey, the [Pg 166] reduction of fertility is inappreciable.

By the term inappreciable I mean that it is not substantially greater than one-tenth of one per cent.—i.e. not more than one-thousandth.

Of course, if the proportion of individuals acquiring the peculiarity is less, the effect on the fertility under the above hypothesis will be greater; and it will not be counteracted so fully unless the number of insect visits is larger, or unless the insects visit more flowers on a journey. Thus if only one-tenth of the race have developed the peculiarity, then, if each flower is visited on the average by five insects who visit five flowers on each trip, the fertility will be reduced about one-third. If, however, the insects visit on the average ten flowers per trip, it will be only diminished about one-tenth; and if they visit fifteen on each trip, it will be only diminished about one-fortieth. If in the same case we suppose that each flower receives ten insect visits, then, if the insects visit on an average five flowers per trip, the fertility will be diminished about one-eighth. If they visit ten on a trip, it will be diminished about one-hundredth, and the diminution is inappreciable if they visit fifteen on a trip. Similarly, if a flower receives fifteen insect visits, the diminution is about one-twenty-fifth, if insects visit on the average five flowers on a trip; and is inappreciable if they visit ten or fifteen.

These figures will show you that it is exceedingly possible that a peculiarity like this, the effect of which at first sight would seem to be so prejudicial to fertility, may in fact have little or no influence upon it; and if you set against this the overwhelming importance of such a peculiarity in segregating the type so as to give it a chance of becoming a fixed species, you will, I think, feel that your hypothesis has nothing to fear from a numerical examination.

I have not examined the case of fertilization by other means; nor have I examined the case of fertilization in animals, where psychological selection can come in. To obtain any useful results, one would have to consider very carefully the circumstances of each case; and at present, at all events, I do not think it would be useful to do so. Nor have I attempted to show the converse of the problem—viz. the effect of swamping where [Pg 167] cross-fertilization is possible. I shall be very glad to examine any one of these cases if you want me to do so; but I should prefer to leave it until I hear from you again.

If you contrast the results that I have given above with those given on pages 181 to 183 of Wallace's book, you will see the enormous difference. His calculations can only apply to the animal kingdom in those cases in which there is only a union between one individual of each sex; and before you can deal with the question of such animals, you will have to take into consideration many elements besides that of mere fertility, if you wish to get any tolerably accurate result[66].

The above analysis leaves nothing to be added by me. But, in conclusion, I may once more repeat that the particular point with which it is concerned is a point of very subordinate importance. For even if Mr. Wallace's computation of chances had been found by Mr. Moulton to have been an adequate computation—and, therefore, even if it had been thus proved that physiological homogamy must always be associated with some other form of homogamy in order to produce specific divergence—still the importance of selective fertility as a factor of organic evolution would not have been at all diminished. For such a result would merely have shown that, not only "in many cases" (as I originally said), but actually in all cases, the selective fertility which I hold to have been so generally concerned in the differentiation of species has required for this purpose the co-operation of some among the numerous other forms of homogamy. But inasmuch as, by hypothesis, no one of these other or co-operating factors would of itself have been capable of effecting specific divergence in any of the cases where its association with selective fertility is

concerned, the mathematical proof that such an association is *always*—and not merely *often*—necessary, would not have materially affected the theory of the origin of species by means of physiological selection. We have now seen, however, that a competent mathematical treatment proves the exact opposite; and, therefore, that Mr. Wallace's criticism fails even as regards the very subordinate point in question. [Pg 168]

APPENDIX C. [Pg 169]

Some Extracts from the Author's Note-books.

Bearing of Weismannism on Physiological Selection.—If in view of other considerations I could fully accept Professor Weismann's theory of heredity, it would appear to me in no small measure to strengthen my own theory of physiological selection. For Weismann's theory supposes that all changes of specific type must have their origin in variations of a continuous germ-plasm. But *the more the origin of species is referred directly to variations arising in the sexual elements, the greater is the play given to the principles of physiological selection*[67]; while, on the other hand, the less standing-ground is furnished to the theory that cross-infertility between allied species is due to "external conditions of life," "prolonged exposure to uniform change of conditions," "structural modifications re-acting on the sexual functions"; or, in short, that "somatogenetic" changes of any kind can of themselves induce the "blastogenetic" change of cross-infertility between progeny of the same parental stock.

Cross-infertility and Diversity of Life.—Observe that one great consequence of duly recognizing the importance of intercrossing is indefinitely to raise our estimate of the part played by the principle of cross-infertility in diversifying organic nature. For whenever in any line of descent the bar of sterility arises, there the condition is given for a new crop of departures (species of a genus); and when genera are formed by the occurrence of this bar, there natural selection and all other equilibrating causes are supplied with new material for carrying on adaptational changes in new directions. Thus, owing to cross-infertility, all these causes are enabled to work out numberless adaptations in many directions (i. e. lines of descent) simultaneously. [Pg 170]

Cross-infertility and Stability.—The importance of sterility as a diagnostic feature is obvious if we consider that more than any other feature it serves to give *stability* to the type; and unless a type is stable or constant, it cannot be ranked as a species. That Darwin himself attributes the highest importance to this feature as diagnostic, see *Forms of Flowers*, pp. 58, 64.

Cross-infertility and Specific Differentiation.—In their elaborate work on the many species of the genus Hieracium, Nägeli and Peter are led to the general conclusion that the best defined species are always those which display absolute sterility *inter se*; while the species which present most difficulty to the systematist are always those which most easily hybridize. Moreover, they find, as another general rule applicable to the whole genus, that there is a constant correlation between inability to hybridize and absence of intermediate varieties, and, conversely, between ability to hybridize and the presence of such varieties.

Cross-infertility in Domesticated Cattle.—Mr. J. W. Crompton, who has had a large experience as a professional cattle-breeder, writes to me (March 2, 1887)—

> "That form of barrenness, very common in some districts, which makes heifers become what are called 'bullers'—that is, irregularly in 'season,' wild, and failing to conceive—is certainly produced by excess of iron in their drinking-water, and I suspect also by a deficiency of potash in the soil."

He also informs me that pure white beasts of either sex are so well known by experienced breeders to be comparatively infertile together, that they are never used for breeding purposes, so that "in some parts of the country, where a tendency to sterility had become so confirmed in the white race that they utterly died out," only the coloured breeds are now to be found. He goes on to say that if "a lot of white heifers were put to a lot of white bulls, I think you would probably get a fertile breed of pure white cattle.... I think, in short, that domestication has produced just what your theory suggests, a new variety inclined to prove sterile with its parent stock." [Pg 171]

Commenting on the origin of domesticated cattle, Professor Oscar Schmidt remarks (*Doctrine of Descent*, p. 139)—

> "Rütimeyer's minute researches on domestic cattle have shown that, in Europe at least, three well-defined species of the diluvial period have contributed to their formation—*Bos primigenius*, *longifrons*, and *frontosus*. These species once lived geographically separate, but contemporaneously; and they and their specific peculiarities have perished, to rise again in our domestic races. These races breed together with unqualified fertility. In the form of skull and horns they recall one or other of the extinct species; but collectively they constitute a new main species. That from their various breeds, the three or any one of the aboriginal species would ever emerge in a state of pristine purity, would be an utterly ludicrous assertion."

Now, seeing that these "aboriginal species," although living "contemporaneously," were

"geographically separate," we can well understand that their divergence of type from a common ancestor did not require, as a condition to their divergence, that any cross-sterility should have arisen between them. The geographical isolation was enough to secure immunity from mutual intercrossing, and therefore, as our present theory would have expected as probable, morphological divergence occurred without any corresponding physiological divergence, as must [Pg 172] almost certainly have been the case if such polytypic evolution had occurred on a common area. Indeed, one of the two lines of experimental verification of our theory consists in selecting cases where nearly allied species are separated by geographical barriers, and proving that, in such cases, there is no cross-sterility.

Fertility of Domesticated Varieties.—Some writers have sought to explain the contrast between domesticated varieties and natural species in respect of fertility when crossed, by the consideration that it is only those natural species which have proved themselves so far flexible as to continue fertile under changed conditions of life that can have ever allowed themselves to become domesticated. But although this condition may well serve to explain the unimpaired fertility under domestication of such species as for this very reason have ever become domesticated, I fail to see how it explains the further and altogether different fact, that this fertility continues unimpaired between all the newly differentiated morphological types which have been derived from the original specific type. It is one thing that this type should continue fertile after domestication: it is quite another thing that fertility should continue as between all its modified descendants, even although the amount of modification may extend much further than that which usually obtains between different natural species.

Testing for Cross-infertility among varieties growing on the same area is a much more crucial line of verification than testing for unimpaired fertility between allied species which occupy different areas, because while in the former case we are dealing with "incipient species" with a view to ascertaining whether the divergence which they have already undergone is accompanied by physiological isolation, in the latter case we can never be sure that two allied species, which are now widely disconnected geographically, have always been so disconnected. They may both [Pg 173] have originated on the same area; or one may have diverged from the other before it migrated from that area; or even if, when it migrated, it was unchanged, and if in its new home it afterwards split into two species by physiological selection, the newer species would probably prove infertile, not only with its parent type, but also with its grand-parent in any other part of the world.

Seebohm on Isolation.—Seebohm is so strongly influenced by the difficulty from "the swamping effects of free intercrossing," that he is driven by it to adopt Asa Gray's hypothesis of variations as teleological. Indeed, he goes as far as Wagner, for he maintains that in no case can there be divergence or multiplication of species without isolation. He makes the important statement that "the more the geographical distribution of birds is studied, the more doubtful it seems to be that any species of bird has ever been differentiated without the aid of geographical isolation" (*Charadriidae*, p. 17). If this is true, it makes in favour of physiological selection by showing the paramount importance of the swamping effects of intercrossing, and consequent importance of isolation. But it makes against physiological selection by showing that the geographical form of isolation is sufficient to explain all the cases of specific differentiation in birds. But I must remember that the latter point rests largely on negative inference, and that birds, owing to their highly locomotive habits, are the class of animals where physiological selection is likely to be most handicapped.

Herbert on Hybridization.—Herbert tells us that when he first astonished the Horticultural Society by laying before them the results of his experiments on hybridization, his brother botanists took serious alarm. For it appeared to them that this "intermixture of species would confuse the labours of botanists, and force them to work their way through a wilderness of uncertainty." Therefore he was bluntly told by several of these gentlemen, "I do not thank you for [Pg 174] your mules." Now, although naturalists have travelled far and learnt much since those days, it appears to me that a modern evolutionist might still turn to the horticulturist with the same words. For assuredly he has no reason to thank the horticulturist for his mules, until he has found a satisfactory answer to the question why it is that natural species differ so profoundly as regards their capacity for hybridizing.

Advance on Herbert's Position.—- If it be said that all my work amounts to showing what Herbert said long ago—viz. that the only true or natural distinction between organic types is the sexual distinction—I answer that my work does much more than this. For it shows that the principle of sterility is the main condition to the differentiation, not merely of species and genera, but also to the evolution of adaptations everywhere, in higher as well as in lower taxonomic divisions. Moreover, even though naturalists were everywhere to consent to abandon specific designations, and, as Herbert advises, to "entrench themselves behind genera," there would still remain the facts of what are now called specific differences (of the secondary or morphological kind), and by whatever name these are called, they alike demand explanation at the hands of the evolutionist.

Fritz Müller on Cross-infertility.—Fritz Müller writes, "Every plant requires, for the production of the strongest possible and most prolific progeny, a certain amount of difference between male and female elements which unite. Fertility is diminished as well when this degree is too low (in relatives too closely allied) as when it is too high (in those too little related)." Then he adds, as a general rule, "Species which are wholly sterile with pollen of the same stock, and even with pollen of nearly allied stocks, will generally be fertilized very readily by the pollen of another species. The self-sterile species of the genus Abutilon, which are, on the other hand, so much [Pg 175]

inclined to hybridization, afford a good example of this theory, which appears to be confirmed also by Lobelia, Passiflora, and Oncidium" (*American Naturalist*, vol. viii, pp. 223-4, 1874).

Different groups of plants exhibit remarkable differences in the capability of their constituent species to hybridize.—In so far as these differences have reference only to first crosses, they have no bearing either for or against my theory. Only in so far as the differences extend to the production of fertile hybrids does any question arise for me. First of all, therefore, I must ascertain whether (or how far) there is any correlation between groups whose species manifest aptitude to form first crosses, and groups where first crosses manifest aptitude to produce fertile hybrids. Next, whatever the result of this inquiry should be, if I find that certain natural groups of plants exhibit comparatively well-marked tendencies to form fertile hybrids, the question will arise, Are these tendencies correlated with *paucity* of species? If they are, the fact would make strongly in favour of physiological selection. For the fact would mean that in these natural groups, owing to "the nature of the organisms" included under them, less opportunity is given to physiological selection in its work of differentiating specific types than is given by other natural groups where the nature of the organism renders them more prone to mutual sterility. But in prosecuting this branch of verification, I must remember to allow for possibilities of differential degrees of geographical isolation in the different groups compared.

On this subject Focke writes me as follows:—"In a natural group (family, order, genus) showing considerable variability in the structure of the flower, we may expect to find [or do find] a greater number of mules than in a group whose species are only distinguished by differences in the shape of the leaves, or in growth, &c. I do not know, however, which in this connexion of things is [Pg 176] the cause and which the effect. A useful ancestral structure of the flower may be conserved by an otherwise varying progeny, on condition that the progress of diversity be not disturbed by frequent intercrossings. [Therefore, if this condition be satisfied, the structure of the flower in different members of the group will continue constant: here the cause of *constancy* in the flower (however much variability there may be in the leaves, &c.) is its original *inability* to hybridize.] On the other hand, in species or groups ready to hybridize [or capable of hybridizing], the fixation of a new specific type will require some change in the structure of the flower, and a change considerable enough to alter the conditions of fertilization. [Here the reason of the *in*constancy of the flower in different members of the group is the original *aptitude* of their ancestral forms to hybridize.] Perhaps there is something in this suggestion, but certainly there are other efficient physiological relations, which are at present unknown. Your theory of physiological selection may serve to explain many difficult facts."

The Importance of Prepotency.—A. Kerner shows by means of his own observations on sundry species of plants which hybridize in the wild state, that they do so very much more frequently if both, or even if only one of the parent forms be rare in the neighbourhood. This fact can only be explained by supposing that, even in species most prone to hybridizing under Nature, there is some degree of prepotency of pollen of the same species over that of the other species; so that where both species are common, it is correspondingly rare that the foreign pollen gets a chance. But if there were no prepotency, the two species would blend; and this Kerner supposes must actually take place wherever two previously separated species, thus physiologically circumstanced, happen to be brought together. (Kerner's paper is published in *Oester. Bot. Zeitschrift*, XXI, 1871, where he alludes to sundry other papers of his own advocating similar views.) [Pg 177]

The relation of these observations to Jordan's *espèces affines* is obvious. We have only to suppose that some such slight and constant difference characterizes the sexual elements of these allied varieties as demonstrably characterizes their morphology, and we can understand how pollen-prepotency would keep the forms distinct—such forms, therefore, being so many records of such prepotency.

Both from Kerner's work, and still more from that of Jordan and Nägeli, I conclude that (at all events in plants) prepotency is the way in which physiological selection chiefly acts. That is to say, *sudden* and *extreme* variations in the way of sexual incompatibility are probably rare, as compared with some degree of prepotency. According as this degree is small or great so will be the amount of the corresponding separation. This view would show that in plants the principle of physiological selection is one of immensely widespread influence, causing (on the same areas) more or less permanent varieties much below specific rank. And when we remember on how delicate a balance of physiological conditions complete correspondency of pollen to ovules depends, we may be prepared to expect that the phenomenon of prepotency is not of uncommon occurrence.

Self-fertilization and Variability.—It occurred to Count Berg Sagnitz that, if physiological selection is a true principle in nature, vegetable species in which self-fertilization obtains ought to be more rich in constant varieties than are species in which cross-fertilization rules. For, although even in the latter case physiological isolation may occasionally arise, it cannot be of such habitual or constant occurrence as it must be in the former case. Acting on this idea, Count Berg Sagnitz applied himself to ascertain whether there is any general correlation between the [Pg 178] habit of self-fertilization and the fact of high variability; and he says that in all the cases which he has hitherto investigated, the correlation in question is unmistakable.

Additional Hypothesis concerning Physiological Selection.—In reciprocal crosses $A \times B$ is often more fertile than $B \times A$. If hybrid AB is more fertile with A, and hybrid BA with B, than vice versa, there would be given a good analogy on which to found the following hypothesis.

Let *A* and *B* be two intergenerating groups in which segregate fecundity is first beginning. Of the hybrids, *AB* will be more fertile with *A*, and *BA* with *B*, than vice versa. The interbreeding of *AB* with *A* will eventually modify sexual characters of *A* by assimilating it to those of *AB*, while the interbreeding of *BA* with *B* will similarly modify sexual characters of *B* by assimilating it to those of *BA*. Consequently, *A* will become more and more infertile with *B*, while *B* becomes more and more infertile with *A*. Fewer and fewer hybrids will thus be produced till mutual sterility is complete.

To sustain this hypothesis it would be needful to prove experimentally, (1) that hybrid forms *AB* are more fertile with *A* than with *B*, while hybrid forms *BA* are more fertile with *B* than with *A* [or, it may be possible that the opposite relations would be found to obtain, viz. that *AB* would be more fertile with *B*, and *BA* with *A*]; (2) that, if so, effect of intercrossing *AB* with *A* is to make progeny more fertile with *A* than with *B*, while effect of intercrossing *BA* with *B* is to make progeny more fertile with *B* than with *A*.

Such experiments had best be tried with species where there is already known to be a difference of fertility between reciprocal crosses (e.g. Matthiola annua and M. glabra, see *Origin of Species*, p. 244).

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FOOTNOTES

[1] It will be remembered that I regard Weismann's theory of heredity, with all its deductive consequences, as still *sub judice*.

[2] *Darwinism*, p. 150.

[3] *The Darwinian Theory, and the Law of Migration* (Eng. Trans., Stanford, London, 1873).

[4] I may here most conveniently define the senses in which all the following terms will be used throughout the present discussion:—*Species* of isolation are, as above stated, homogamy and apogamy, or isolation as discriminate and indiscriminate. *Forms* of isolation are modes of isolation, such as the geographical, the sexual, the instinctive, or any other of the numerous means whereby isolation of either species may be secured. *Cases* of isolation are the instances in which any of the forms of isolation may be at work: thus, if a group of *n* intergenerants be segregated into five groups, *a*, *b*, *c*, *d*, *e*, then, before the segregation there would have been one case of isolation, but after the segregation there would be five such cases.

[5] *Divergent Evolution through Cumulative Segregation* (*Zool. Journal, Linn. Soc.*, vol. xx. pp. 189-274).

[6] The passage proceeds to show that in view of this consideration we have a strong additional reason for rejecting the *a priori* dogma that all specific characters must necessarily be useful characters. For it is evident that any divergence of specific character which is brought about in this way need not present any utilitarian significance —although, of course, natural selection will ensure that it shall never be deleterious.

[7] *Revue Scientifique*, Nov. 23, 1889.

[8] *Nature*, Oct. 10, 1889, p. 568.

[9] e. g. p. 81.

[10] See Chapter xxiii. vol. ii. p. 262. (Edition of 1888.)

[11] This term may here be taken as equivalent to Isolation.

[12] *Zool. Journal Lin. Soc.*, vol. xix. pp. 337-411.

[13] *Ibid.*, vol. xx. pp. 202-212.

[14] *Zool. Journal Lin. Soc.*, vol. xxiii. p. 313.

[15] *See Nineteenth Century*, January, 1887, pp. 61, 62.

[16] *Nicaragua*, p. 207.

[17] *Nature*, vol. xxxi. p. 4.

[18] *Zool. Journal, Lin. Soc.*, vol. xix. pp. 337-411 (1886); and for Mr. Gulick's papers, *ibid.*, vol. xx. pp. 189-274 (1887), vol. xxiii. pp. 312-380 (1889). Mr. Gulick has recently drawn my attention, in a private letter, to the fact that as early as 1872 a paper of his was read at the British Association, bearing the title *Diversity of Evolution under one set of External Conditions*, and that here the principle of physiological segregation is stated. Although it does not appear that Mr. Gulick then appreciated the great importance of this principle, it entitles him to claim priority.

[19] *Darwinism*, p. 169.

[20] *Origin of Species*, p. 136.

[21] *Darwinism*, p. 152.

[22] *Origin of Species*, pp. 44, 45.

[23] *Origin of Species*, ed. 6, pp. 134, 135.

[24] *Archives des Sciences physiques et naturelles* (Genève), vol. liii. (1875), pp. 211-236.

[25] *Remarques sur le fait de l'existence en société à l'état sauvage des espèces végétales affines et sur d'autres faits relatifs à la question de l'espèce*, par Alexis Jordan; lues au congrès de l'Association Française pour l'Avancemeat des Sciences, 2^{m}e session, Lyon, séance de 28 Août, 1873.

[26] *Evolution and its Relations to Religious Thought*, &c. pp. 236-7.

[27] *Life and Letters*, vol. ii. p. 28.

[28] *Ibid.*

[29] *Origin of Species*, p. 80, 6th ed. (1872).

[30] *Life and Letters*, vol. iii. p. 158.

[31] *Ibid.* p. 159.

[32] *Ibid.* p. 160.

[33] The analogy is radically unsound because unconscious selection differs from methodical selection only in the *degree* of "separation" which it effects. These two forms of selection do not necessarily differ from one another in regard to the *number* of characters which are being simultaneously diversified; for while it may be the object of methodical selection to breed for modification of a single character alone, it may, on the other hand, be the result of unconscious selection to diversify an originally uniform stock, as Darwin himself observes with regard to horse-breeding. The real distinction between monotypic and polytypic evolution is, not at all with reference to the *degree* of isolation (i. e. *amount* of "separation"), but to the *number of cases* in which any efficient degree of it occurs (i. e. whether in but a single case, or in two or more cases).

[34] *Life and Letters*, vol. iii. pp. 157-8.

[35] *Ibid.* pp. 157-8.

[36] *Life and Letters*, vol. iii. p. 161.

[37] Page 81. The three forms of isolation mentioned are, "from haunting different stations, from breeding at slightly different seasons, or from the individuals of each variety preferring to pair together."

[38] *Life and Letters*, vol. iii. p. 159.

[39] *Life and Letters*, vol. iii. p. 155.

[40] *Variation*, &c., vol. ii. p. 262.

[41] *Life and Letters*, vol. iii. p. 161.

[42] *Die Darwin'sche Theorie und das Migrationsgesetz* (1868): *Ueber den Einfluss der geographischen Isolirung*, &c. (1870).

[43] For instance, speaking of common, or continuous areas, he says:—"In this case a constant variety, or new species, cannot be produced, because the free crossing of a new variety with the old unaltered stock will always cause it to revert to the original type; in other words, will destroy the new form. The formation of a real variety, which Darwin, as we know, regards as the commencement of a new species, will only succeed when a few individuals, having crossed the barrier of their habitat, are able to separate themselves for a long time from the old stock." And the last sentence, given as a summary of his whole doctrine, is—"The geographical isolation of the form, a necessary consequence of migration, is the cause of its typical character."

[44] *Ueber den Einfluss der Isolirung auf die Artbildung* (1872).

[45] *Loc. cit.*, p. 43.

[46] *Physiological Selection*, pp. 348, 389.

[47] *Loc. cit.*, p. 54.

[48] *Nature*, vol. xliii. p. 410, and vol. xliv. p. 29.

[49] *Darwinism*, p. 143.

[50] In Appendix to H. M. Stanley's *How I found Livingstone*, 2nd ed. London, 1872, p. 715.

[51] *Animal Life and Intelligence*, pp. 98, 99 (1890-1891).

[52] *The Factors of Evolution* (1891).

[53] *Darwinism*, p. 151.

[54] *Ibid.*

[55] *Loc. cit.*, p. 151.

[56] Namely, *Lycaena denzelii*, *L. pheretes*, *Argynnis pales*, *Erebia mante*.

[57] Since the above was written, I have heard of some cases which seem to present greater difficulties to our theory than those above quoted. These refer to some of the numerous species of land mollusca which inhabit the isolated rocks near Madeira (Dezertas). My informant is Dr. Grabham, who has himself investigated the matter, and reports as follows:—

"It is no uncommon thing to meet with examples of the same species, sub-fossil, recent, and living upon one spot, and presenting no variation in the long record of descent." Then, after naming these examples, he adds, "All seem to vary immediately on attaining new ground, assuming many aspects in different districts."

Unquestionably these statements support, in a very absolute manner, Mr. Wallace's opinion, while making directly against my own. It is but fair, however, to add that the cases are not numerous (some half-dozen at the most, and all within the limits of a single genus), and that, even in the opinion of my informant himself, the facts have not hitherto been sufficiently investigated for any decisive judgement to be formed upon them.

[58] Vol. xliii. p. 127.

[59] This refers to what I understand Mr. Wallace to say in the *Nature* correspondence is the supposition on which his own theory of the origin of species by cross-infertility is founded. But in the original statement of that theory itself, it is everywhere "supposed"

that when species are originated by cross-infertility, the *initial* change *is* the physiological change. In his original statement of that theory, therefore, he literally went further than I had gone in my "original paper," with reference to supposing the physiological change to be the initial change. I do not doubt that this is due to some oversight of expression; but it is curious that, having made it, he should still continue his endeavour to fix exactly the same oversight upon me.

[60] "Positive segregation" is Mr. Gulick's term for forms of homogamy other than that which is due to selective fertility. Of these other, or "positive" forms, natural selection is one; but as it is far from being the *only* one, the criticism points out that utility is not the *only* conserving principle with which selective fertility may be associated.

[61] By Intensive Segregation Mr. Gulick means what I have called Independent Variability.

[62] His sentence, "all fertility not correlated with some *useful* variation has a constant tendency to effect its own elimination," still further restricts the possible action of physiological selection to cases where at least one of the other forms of homogamy with which it is associated is natural selection. Or, in other words, it is represented that physiological selection must always be associated with natural selection, even if it be likewise associated with any other form of exclusive breeding. But as this further limitation appears to me self-evidently unjustifiable (seeing that utility is not the only possible means of securing effective isolation) I here neglect it, and take the wider ground marked out above. It is needless to say that this is giving Mr. Wallace every possible advantage, by not holding him to his still narrower ground.

[63] In our *Nature* correspondence of 1890-1891, Mr. Wallace remarked: "If Dr. Romanes will carefully work out numerically (as I have attempted to do) a few cases showing the preservative and accumulative agency of pure physiological selection within an otherwise undifferentiated species, he will do more for his theory than volumes of general disquisition or any number of assertions that it *does* possess this power." Several months before this was written I had already in my hands Mr. Moulton's letter, with its accompanying calculations.

[64] As, for example, in the case of sexuality in general. It is not to the advantage of such individual male Arthropoda as perish after the performance of the sexual act that they should perform it; but its performance is necessary for the perpetuation of their species. —G. J. R.

[65] In this anticipation Mr. Moulton is right. The well-known botanist, Mr. Bennett, read a most interesting paper on the subject before the British Association in 1881. His results have since been corroborated by other observers. In particular, Mr. R. M. Christy has recorded the movements of 76 insects while visiting at least 2,400 flowers. (*Entomologist*, July 1883, and *Zool. Journal Lin. Soc.*, August 1883.) The following is an analysis of his results. In the case of butterflies, in twelve observations on nearly as many species, there are recorded altogether 99 visits to fifteen species of flowers; and of these 99 visits 94 were constant to the same species, leaving only 5 visits to any other, or second species. In the case of the hive-bee, there were 8 individuals observed: these visited altogether 258 flowers, and all the visits paid by the same individual were paid to the same species in each of the eight cases. Lastly, as regards bumble-bees, there were altogether observed 55 individuals belonging to four species. These paid altogether 1751 visits to 94 species of flowers. Of these 1751 visits, 1605 were paid to one species, 131 to two species, 16 to three, 6 to four, and 1 to five. Adding all these results together, we find that 75 insects (butterflies and bees) visited 117 species of flowers: of these visits, 1957 were constant to one species of flower; 136 were paid also to a second species, 16 also to a third, 6 also to a fourth, and 1 also to a fifth. Or, otherwise stated, while 1957 were absolutely constant, from such absolute constancy there were only 159 deviations. Moreover, if we eliminate three individual humble bees, which paid nearly an equal number of visits to two species (and, therefore, would have ministered to the work of physiological selection almost as well as the others), the 159 deviations become reduced to 72, or about four per cent. of the whole.—G. J. R.

[66] Here follows the Appendix presenting the calculations on which the above results are founded; but it seems unnecessary to reproduce it on the present occasion.—G. J. R.

[67] *Doctrine of Descent and Darwinism*, Eng. trans. p. 139.

Transcriber's Notes

In paragraph 4 of page 171 "peculiarites" has been corrected to "peculiarities"

Variable spacing in the following abbreviation was left as it was in the original: "i. e." (22 instances) and "i.e." (14 instances).

Different hyphenation patterns were left as in the original text:

prepotent (1 instance)	pre-potent (1 instance)
presupposes (1)	pre-supposes (1)
reacting(5)	re-acting (1)
restatement (1)	re-statement (2)
superinduced (2)	super-induced (1)

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