Divergent Evolution through Cumulative Segregation.

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INTRODUCTION.

IN my study of Sandwich-Island terrestrial mollusks my attention was early arrested by the fact that wide diversity of allied species occurs within the limits of a single island, and in districts which present essentially the same environment. As my observations extended, I became more and more impressed with the improbability that these divergences had been caused by differences in the environment. It was not easy to prove that sexual selection had no influence; but, owing to the very low grade of intelligence possessed by the creatures, it seemed impossible that the form and colouring of the shells should be the result of any such process. I was therefore led to search for some other cause of divergent transformation, the diversity of whose action is not dependent on differences in nature external to the organism.

I found strong proof that there must be some such principle, not only in the many examples of divergence under uniform activities in the environment, but in the fact that the degrees of divergence between nearly allied forms are roughly measured by the number of miles by which they are separated, and in the fact that this correspondence between the ratios of distance and the ratios of divergence is not perceptibly disturbed by passing over the crest of the island into a region where the rainfall is much heavier, and still further in the fact that the average size of the areas occupied by the species of any group varies, as we pass from group to group, according as the habits of the group are more or less favourable to migration. I perceived that these facts could all be harmonized by assuming that there is some cause of divergence more constant and potent than differences in nature external to the organism; and that the influence of this cause was roughly measured by the time and degree of separation.

During the summer of 1872 I prepared two papers in which these facts and opinions were presented. One of these, entitled "The Variation of Species as related to their Geographical Distribution, illustrated by the Achatinellinæ," was published in

'Nature' for July 18, 1872; the other, entitled "Diversity of Evolution under one Set of External Conditions," after being read before the British Association for the Advancement of Science in August 1872, was, through the kindness of Mr. Alfred Wallace, brought before the Linnean Society, and was finally published in the Linnean Society's Journal, Zoology, vol. xi. pp. 496–505.

In the former paper I used the following words in calling attention to the impossibility of explaining the origin and distribution of these forms by Natural Selection. "Whether we call the different forms species or varieties, the same questions are suggested as to how they have arisen and as to how they have been distributed in their several localities. In answering these questions, we find it difficult to point to any of those active causes of accumulated variation, classed by Darwin as Natural Selection. . . . . There is no reason to doubt that some varieties less fitted to survive have disappeared; but it does not follow that the 'Survival of the Fittest' (those best fitted when compared with those dying prematurely, but equally fitted when compared with each other) is the determining cause which has led to these three species being separated from each other in adjoining valleys. *The 'Survival of the Fittest' still leaves a problem concerning the distribution of those equally fitted.* It cannot be shown that the 'Survival of the Fittest' is at variance with the survival, under one set of external circumstances, of varieties differing more and more widely from each other in each successive generation. The case of the species under consideration does not seem to be one in which difference of environment has been the occasion of different forms being preserved in the different localities. It is rather one in which varieties resulting from some other cause, though equally fitted to survive in each of the localities, have been distributed according to their affinities in separate localities."

In the latter paper I raised the following questions concerning Natural Selection. "The terms 'Natural Selection' and 'Survival of the Fittest' . . . . imply that there are variations that may be accumulated according to the differing demands of external conditions. What, then, is the effect of these variations when the external conditions remain the same? Or, can it be shown that there is no change in organisms that is not the result of change in external conditions? Again, if the initiation of change in the organism is through change in the environment, . . .

does the change expend itself in producing from each species just one new species completely fitted to the conditions, *or may it produce from one stock many that are equally fitted?*" (p. 497). In answering these questions I called "attention to the variation and distribution of terrestrial mollusks, more especially those found on the Sandwich Islands," and gave what seemed to me strong reasons for believing that "*The evolution of these different forms cannot be attributed to difference in their external conditions.* . . . If we would account for the difference and the limited distribution of these allied forms on the hypothesis of evolution from one original species, *it seems to me necessary to suppose two conditions, Separation and Variation.* I regard *Separation* as a condition of the species, and not of surrounding nature, because it is a state of division in the stock which *does not necessarily imply any external barriers, or even the occupation of separate districts. This may be illustrated by the separation between the castes of India, or between different genera occupying the same locality.* . . . We must suppose that they [the diverging forms] must possess an inherent tendency to variation so strong that *all that is necessary to secure a divergence of types* in the descendants of one stock *is to prevent*, through a series of generations, *their intermingling* with each other to any great degree" (pp. 498–499). I also called attention to the fact that some forms of Natural Selection must "prevent variation and give a wider diffusion to forms that would otherwise be limited in their range and variable in their type. Natural Selection is as efficient in producing permanence of type in some cases as in accelerating variation in other cases" (p. 504). On page 499 I pointed out the law that "The area occupied by any species must vary directly as its power and opportunity for migration, and inversely as its power of [divergent] variation." And on page 505 I gave a brief summary of my reasons for believing that "*Separation without a difference of external circumstances is a condition sufficient to ensure . . . divergence in type.*"

Subsequent investigation has led to the development of my theory, with a fuller discussion of the causes and laws that are revealed in these phenomena. In an article published in 'The Chrysanthemum' (Yokohama and London, Trübner & Co.), January 1883, I state my belief "that the quality, the diversity, and the rapidity of the variation depend chiefly upon the nature of the organism; and that while the nature of the external

conditions has power to winnow out whatever forms are least fitted to survive, *there will usually remain a number of varieties equally fitted to survive*; and that *through* the *law of segregation* constantly operating in species distributed over considerable areas, *these varieties continue to diverge* both in form and in habits till separate species are fully established, though the conditions are the same throughout the whole area occupied by the diverging forms." The conclusion reached was, that "The theory that diversity of Natural Selection is, like variation, an essential factor in producing diversity of species, is untenable. On the contrary, we find that diversity of Natural Selection is not necessary to diversity of evolution, nor uniformity of Natural Selection to uniformity of evolution; but while *variation and separation are the essential factors in diversity*, and intercrossing and unity of descent the essential agents in uniformity of *evolution*, Natural Selection may be an important ally on either side."

In an article on "Evolution in the Organic World," published in 'The Chinese Recorder' (Shanghai), July 1885, I use the following language:—"We see what Natural Selection cannot explain by considering the nature of the process. The survival of the fittest results in the separate breeding of the fittest, and therefore in the increasing fitness of successive generations of survivors; *but how can it account for the division of the survivors of one stock, occupying one country, into forms differing more and more widely from each other? To explain such a result we must find some other law. I am prepared to show that there is such a law rising out of the very nature of organic activities, a law of Segregation, bringing together those similarly endowed, and separating them from those differently endowed.*"

Without Variation there can be no Segregate Breeding; and without Segregate Breeding and Heredity there can be no accumulation of divergent variations resulting in the formation of races and species. In producing divergent evolution, the causes of Variation and Heredity are therefore as important as the causes of Segregate Breeding; and though I pass them by in my present discussion, I trust it will not be attributed to an underestimate of their importance. Though I do not stop to discuss the causes of variation, my reasoning rests on the observed fact that in every department of the organic world variation is found, and that in the vast majority of cases, if not absolutely in all, the diversities to which any freely intergenerating group of

organisms is subject follow the general law of "Frequency of Deviation from an Average." As this is a law according to which half of the members of the intergenerating group are above and half below the average in relation to any character, there must often occur simultaneous variation of several individuals in some character which tends to produce Segregate Breeding. The reality and importance of this law is not at all dependent on the reality of any of the theories of heredity and variation that are now being discussed. Whatever may be the causes that produce variation, whether they depend entirely upon changes in external conditions, or are chiefly due to changing activities in the organism and the hereditary effects of acquired characters, or are, as Weismann maintains, the direct result of sexual reproduction which never transmits acquired characters,—in any and every case this law of Deviation from an Average remains undisturbed, and is recognized as an important factor in the present paper. It therefore cannot be urged that the theory here advanced assumes simultaneous variation without any ground for making such an assumption; nor can it be said that it rests on the incredible assumption that chance variation of very rare kinds will be duplicated at one time and place, and will represent both sexes.

Moritz Wagner first discussed what he calls "The law of the migration of organisms" in a paper read before the Royal Academy of Sciences at Munich, in March 1868; but my attention was not called to it till after the reading of my paper before the British Association in August 1872. In a fuller paper entitled "The Darwinian Theory and the Law of the Migration of Organisms," an English translation of which was published by Edward Stanford (London, 1873), the same author maintains that "the constant tendency of individuals to wander from the station of their species is absolutely necessary for the formation of races and species" (p. 4). "The migration of organisms and their colonization are, according to my conviction, a necessary condition of natural selection" (p. 5). On pp. 66 and 67 he expands the same statement, and objects to Darwin's view "that on many large tracts all individuals of the same species have become gradually changed." Again, he contends that "Transformation is everywhere and always dependent on isolation in order to have lasting effect. Without separation from the home of the species, this wonderful capacity would be completely

neutralized" (p. 74). "Natural Selection is not in itself an unconditional necessity, but is dependent on migration and geographical isolation during a long period, together with altered conditions of life" (p. 57). "Where there is no migration, that is where no isolated colony is founded, natural selection cannot take place" (p. 59).

A comparison of his paper with my two papers published in 1872, already referred to, will show several fundamental differences in the two theories. He maintains that:—

(1) The separation of a few individuals from the rest of the species is absolutely necessary for the operation of Natural Selection, and therefore for any transformation of the species, no matter how great the change of conditions may be in the original home of the species.

(2) Migration and geographical barriers are the only effectual causes, independent of human action, by which a few individuals can be separated from the rest of the species, and are, therefore, necessary to the transformation of species.

(3) Exposure to a new form of Natural Selection is a necessary condition for any transformation of a species.

(4) Difference of external conditions is necessary to difference of Natural Selection, and therefore necessary to any transformation of species.

(5) Geographical isolation and altered conditions of life are necessary conditions for Natural Selection, as that is for the modification of species.

(6) The separation of which he speaks is the entering of a few individuals into a new territory, where the conditions are different from those in the old habitat, and where the body of the species fail of reaching them.

My chief positions were the following, in strong contrast with the foregoing:—

(1) Separate generation is a necessary condition for divergent evolution; but not for the transformation of all the survivors of a species in one way.

(2) "Separation does not necessarily imply any external barriers, or even the occupation of separate districts."

(3) Diversity of Natural Selection is not necessary to diversity of evolution.

(4) Difference of external conditions is not necessary to diversity of evolution.

(5). "Separation and Variation," that is, Variation not overwhelmed by crossing, "is all that is necessary to secure a divergence of types in the descendants of one stock," though external conditions remain the same, and though the Separation is other than geographical.

(6) The Separation of which I speak is anything, in the species or in the environment, that divides the species into two or more sections that do not freely intercross, whether the different sections remain in the original home or enter new and dissimilar environments.

Though these propositions were very briefly and imperfectly presented, I am not aware that any better statement of the facts of Segregation had been previously published.

The present paper is the result of a long continued endeavour to understand the relations in which this factor stands to Natural Selection and the other causes that co-operate in producing divergent evolution; and though my work has been done under the great disadvantage of entire separation from libraries, and from other workers in similar lines, I trust it may contribute something towards the elucidation of the subject. In expanding my theory I have been unable to make any use of the positions taken in Moritz Wagner's paper, as they seem to me very extreme and far removed from the facts of nature. The two theories correspond chiefly in that they discuss the relation of Separation to the transformation of species; while the explanations given of the nature, causes, and effects of Separation widely differ. I am informed that my paper on "Diversity of Evolution under One Set of External Conditions" was translated and circulated in Germany; but whether it had any effect in modifying Wagner's theory, I have not the means of knowing.

I have recently discovered that the principle of Segregate Breeding, which I have found to be of such importance in the evolution of species, is allied to the law of Segregation propounded by Spencer in his 'First Principles.' By direct consideration of the conditions that have been found necessary for the development of divergent races of domestic plants and animals, I have discovered Segregate Breeding as a necessary condition for divergent evolution; and by direct observation on the propagation of plants and animals under natural conditions, I have discovered Cumulative Segregation as a constant result from certain forms of activity in the organism when dealing with a

complex environment; it is therefore with special pleasure that I observe that a law of very similar import may be derived by a wholly different method from the general laws of action and reaction in the physical world. It should, however, be noticed that in the brief references made to the subject in Spencer's 'Principles of Biology'* it is assumed that "Increasingly-definite distinctions among variations are produced wherever there occur definitely-distinguished sets of conditions to which the varieties are respectively subject," and only where these occur; for "Vital actions remain constant so long as the external actions to which they correspond remain constant;" and no reference is anywhere made to the principle that whatever causes sexual separation between dissimilar members of one family, race, or species tends not only to perpetuate, but to increase their dissimilarity in the succeeding generations. The view maintained in the following paper is, I believe, in better accord with the fundamental principle that "Unlike units of an aggregate are sorted into their kinds and parted when uniformly subject to the same incident forces,"† as is also the teaching of Spencer's 'Principles of Biology' in one passage; for I have recently discovered that in a single paragraph of this work it is maintained that, while exposed to the same external conditions, the members of the same species may be increasingly differentiated, "until at length the divergence of constitutions and modes of life become great enough to lead to segregation of the varieties."‡ If the segregation had been introduced as a necessary condition without which the divergence of families and races could not take place, the position taken in this paragraph would have been essentially the same as the one I have adopted. In the next section, however, he abandons the position, using the following words:—"Through the process of differentiation and integration which of necessity brings together, or keeps together, like individuals, and separates unlike ones from them, *there must nevertheless be maintained a tolerably uniform species, so long as there continues a tolerably uniform set of conditions in which it may exist.*" [The italics are mine.]

I trust my endeavour to contribute something toward the development of the theory of divergent evolution will not be

* Compare §§ 91, 156, 169, 170.

† See Spencer's 'First Principles,' § 166, near the end; also a fuller statement in § 169.

‡ See § 90.

attributed to any lack of appreciation of what has already been accomplished. The propounders of a doctrine which has profoundly influenced every department of modern thought need no praise from me; but as their theory is confessedly incomplete, and as one of the leaders in the movement has called attention to the need of a rediscussion of the fundamental factors of evolution, I offer my suggestions and amendments after prolonged and careful study.

Physiological Selection and Segregate Fecundity.

The abstract of Mr. Romanes's paper on "Physiological Selection," given in 'Nature' August 5th, 12th, and 19th, 1886, did not come into my hands till the following January, when my theory of Divergent Evolution through Cumulative Segregation, which had been gradually developing since the publication of my paper on "Diversity of Evolution under One Set of External Conditions," was for the most part written out in its present form. Since then, and with reference to the discussion on Physiological Selection, I have worked out the algebraic formulas given in the last chapter, and have introduced explanations of the same; but at the same time I have removed several chapters in which the principle of selection was discussed at length, and have endeavoured to bring the whole within a compass that would allow of its being published by some scientific society. In order to attain this end, I reserve for another occasion a discussion of the principles of Intensive Segregation, under which name I class the different ways in which other principles combine with Segregation in producing Divergent Evolution.

It was my intention to bring together examples of the different forms of Segregation discussed, that they might be published with the theoretical part; but the large number of pages found necessary for even the briefest presentation of the principles involved, and the fact that Mr. Romanes's paper has appeared relating to some of the same problems, leads me to present the results of my studies without further delay. The facts on which large portions of my theory rest are of the most familiar kind, and no additional light would be gained though their numbers were multiplied a hundredfold. Indeed one of the marked features of my theory is that in its chief outlines it rests on facts that are universally acknowledged. The aim of the

theory is to show the connection of these facts with divergent evolution.

Though many divergences appear in our method of treating the subject, the fundamental theory underlying my Segregate Fecundity and Mr. Romanes's Physiological Selection seems to be very similar, if not the same. The most important differences I have noticed are, (1) that he seems to regard mutual sterility as sufficient to account for the separate propagation of species and varieties thus characterized, without calling in the aid of any other form of segregation, while I regard it as a Negative form of Segregation that would result in the general destruction of all life if not associated with what I call Positive forms of Segregation; and (2) that he maintains that "Physiological selection is almost exclusively a theory of the origin of species, seeing that it can but very rarely have had anything to do with the formation of genera, and can never have had anything at all to do with the formation of families, order, or classes. Hence, the evidence which we have of the evolutionary influence of physiological selection, unlike that which we have of the evolutionary influence of natural selection, is confined within the limits of specific distinctions," * while I maintain that Segregation of some form is a necessary condition for all divergent evolution, and that in fact Segregate Fecundity in many cases prevents the intercrossing of divergent forms that, though descended from a common stock, now belong to different families and orders.

The first of these differences, though of considerable importance, is, I think, due to the method of presentation, rather than to any fundamental discrepancy in the theories. The Positive forms of Segregation are, I judge, assumed to be present, though their co-operation is not distinctly recognized as a necessary condition for the breeding of forms that are mutually sterile.

I must, however, confess that I do not see how to reconcile his statement that "Physiological selection can never have had anything at all to do with the formation of families, orders, or classes" with what I believe to be the facts concerning Segregate Fecundity; and if physiological selection is to be understood as including Seasonal and perhaps other forms of Segregation, this passage seems to be still more opposed to the principles of divergent evolution as I understand them. He certainly could not have intended to say that mutual fertility between allied

* Linn. Soc. Journ., Zoology, vol. xix. p. 396.

genera not otherwise segregated would not have stood in the way of their becoming different families, and that therefore mutual sterility has had nothing to do with their continued divergence; still he seems to have failed to perceive the important influence this principle must have had on the divergent evolution of the higher groups of organisms.

The correspondences in the two papers are notwithstanding more remarkable than the differences. Of these, the most conspicuous is the use of the word Segregation to express the principle under consideration.* As I have already pointed out, I used this word for the same purpose in an article in the 'Chrysanthemum,' published in January 1883; and again in the 'Chinese Recorder' for July 1885, where I spoke of the "Law of Segregation rising out of the very nature of organic activities, bringing together those similarly endowed," and causing "the division of the survivors of one stock, occupying one country, into forms differing more and more widely from each other."

I trust that my discussion of the various forms of Segregation, both Negative and Positive, though presented in so condensed a form, will throw light on the subject of the mutual sterility of species; and that in other ways my presentation of the subject will contribute something, not only to the theory of Physiological *Segregation*, but to other branches of the general theory of evolution.

I should here acknowledge (what will, I think, be manifest on every page of my paper) that my obligations to Darwin and Wallace are far greater than are indicated by quotations and references.

I very much regret that I have failed of obtaining a copy of 'Evolution without Natural Selection,' by Charles Dixon; but, from his letter in 'Nature,' vol. xxxiii. p. 100, I see that he maintains "That isolation can preserve a non-beneficial variation as effectually as natural selection can preserve a beneficial variation." He does not there refer to the fact, which I emphasize, that all divergence of a permanent character, whether beneficial or non-beneficial, is dependent on Segeneration either Separative or Segregative.

* See paper on "Physiological Selection," Linn. Soc. Journ., Zoology, vol. xix. pp. 354, 356, 391, 395.

Preliminary Definitions.

Believing that great obscurity has often been introduced into the discussion of biological subjects by the use of terms of uncertain import, I have endeavoured to obtain greater precision by giving definitions of the terms I have introduced; and for the sake of indicating what words are thus used with special and definite meanings, they have been distinguished by capitals. A few of these definitions are here given, and others will be given in the body of the paper.

An Intergenerant, or *Intergenerating Group*, is a group of individuals so situated and so endowed that they freely cross with each other.

Segeneration, or *Independent Generation*. In harmony with the fundamental doctrines of evolution, I assume that each species was at one time a single intergenerant; but we find that many species are now divided into two or more intergenerants, between which there is little or no intercrossing. This state of freedom from crossing I call Segeneration. Segeneration is of two kinds, Separate Generation and Segregate Generation.

Separate Generation, or *Separation*, is the indiscriminate division of a species into groups that are prevented from freely crossing with each other.

Segregate Generation, or *Segregation*, is the intergeneration of similar forms and the prevention of intergeneration between dissimilar forms.

Select Generation, or *Selection*, is the partial or complete exclusion of certain forms from the opportunity to propagate, while others succeed in propagating. The generation of any form is *select* with reference to the non-generation of forms that fail of propagating, and *segregate* with reference to the generation of forms that propagate successfully, but separately.

Adaptational Selection is exclusive generation that depends upon superior adaptation either to the environment or to other members of the same species.

Natural Selection is the exclusive generation of those better fitted to the natural environment, resulting from the failure to generate of those less fitted.

Artificial Selection is the exclusive generation of those better fitted to the rational environment.

Reflexive Selection is the exclusive generation of those better

fitted to the relations in which the members of the same species stand to each other. Sexual, Social, and Institutional Selection are forms of Reflexive Selection.

The Environment is nature lying outside of the Intergenerant. The influence of the Environment is the sum of the influences that fall upon the members of an Intergenerant, exclusive of their influence upon each other. The environment of an intergenerant includes members of the same species, only when these members are so near that they exert an influence through competition or otherwise, while at the same time they are so far differentiated that they do not intercross; in other words, the members of the same species can mutually belong to the environment, only when they have acquired some of the characteristics of independent species. The same environment extends as far as the activities that affect or may affect the species extend without undergoing change.

Change in the Environment is change in the external activities affecting the species.

Entering a new Environment is change in the territorial distribution of the species, bringing either all or a portion of its members within the reach of new influences. This may also be called *Change of Environment.*

Change in the Organism, whether producing new adaptations to the environment or not, should be carefully distinguished from both of the above described changes.

Change of Relations to the Environment may be produced by Change in the Environment, or by Entering a new Environment, or by Change in the Organism.

As great confusion has been occasioned by the terms "Conditions of Life" and "External conditions" being used, sometimes for activities outside of the species under consideration, and sometimes for those within the species (as for example the influence upon the seed produced by its position in the capsule), I have tried to avoid their use.

Monotypic Evolution is any transformation of a species that does not destroy its unity of type.

Polytypic Evolution or *Divergent Evolution* is any transformation of a species in which different types appear in different sections.

CHAPTER I.

The Effects of Selection and Independent Generation Contrasted.

In as far as any theory of evolution fails of giving an explanation of divergence of character, in so far it fails of explaining the origin of species. This is the crucial test which must decide the strength or weakness of every theory that is brought forward to account for the derivation of many species from one original species. A satisfactory theory will not only point out the conditions on which divergence depends, but will show that these conditions are the natural result of causes that are already recognized by science as having influence in the organic world, or that are now shown to have such influence.

In the present chapter I shall present some reasons for believing that neither "Natural Selection," nor "Sexual Selection," nor "the Advantage of Divergence of Character," nor "Difference of External Conditions," nor all these taken together, nor any form of Selection that may be hereafter discovered, is sufficient to account for Divergence of Character, but that another factor of equal if not superior importance must be recognized. In subsequent chapters I shall try to trace the causes on which this additional factor depends, and to indicate as far as possible the laws and relations under which they appear.

Divergent Evolution not explained by Natural Selection.

Natural Selection is the exclusive generation of certain forms through the failure to live and propagate of other kinds that are less adapted to the environment.

In the case of the breeder, no selection avails anything that does not result in some degree of exclusion. In the case of natural selection, where we are not considering ineffectual intentions, the selection is measured by the exclusion. Where there is no exclusion, there is no selection, and where the exclusion is great the selection is severe. Moreover, it is self-evident that there can be no crossing between the best fitted that survive and propagate, and the least fitted that perish without propagating. To this extent, therefore, the prevention of crossing is complete. And further, it is evident that those whose meagre fitness gives them but little opportunity for propagating will have a correspondingly

diminished opportunity for crossing with the best fitted; and so on through the different grades of fitness, the power to affect the next generation through having a share in propagating will measure the power to affect the progeny of the best fitted by crossing with them. It therefore follows that the freest crossing of the fittest is with the fittest.

Natural Selection therefore proves to be *a process in which the fittest are prevented from crossing with the less fitted through the exclusion of the less fitted*, in proportion to their lack of fitness. Through the premature death of the least fitted, and the inferior propagation of the less fitted, there arises a continual prevention of crossing between the less fitted and the better fitted; and without this separation the transforming influence of the laws of organic life would have no power to operate. As Darwin has pointed out, the results produced by this removal of the less fitted and separate propagation of the better fitted, closely correspond with those produced by the breeder, who kills off the less desirable individuals of his stock before they have opportunity to breed. The selection of the breeder avails nothing unless it leads to the determining of the kind that shall breed; and this he cannot accomplish without preventing free crossing with those that he does not desire. He must use some method to secure the separate breeding of the form that he desires to propagate. We therefore find in both Natural and Artificial Selection the same fundamental method. In either case, the kind that is to propagate is determined by the selection, and those that are not to propagate are in some way excluded. The process may therefore be called the exclusive breeding of certain kinds; and *Natural Selection* may be defined as *the exclusive breeding of those better adapted to the environment.*

But if from one stock of horses we wish to develop two distinct breeds, one of which shall excel in fleetness, and the other in strength for carrying or drawing burdens, the result will not be gained by simply preventing all that are inferior in strength or fleetness from breeding. By this process, which is the Exclusive Breeding of the desired kinds, we should obtain one breed with fair powers of strength and fleetness; but the highest results in either respect would not be gained. *Such experiments show that the Exclusive Breeding of other than average forms causes Monotypic Evolution, and that to secure Divergent or Polytypic Evolution some other principle must be introduced.*

In the case of Natural Selection, the separation it introduces is between the living and the dead, between the successful and the unsuccessful. In other words, Natural Selection is the exclusion of all the forms that through lack of adaptation to the environment fail of leaving progeny, and therefore in the exclusive generation of the forms that through better adaptation to the environment are better able to propagate. *Variation with the Natural Selection of other than average forms may therefore account for the transformation of an ancient species into a series of successive species* the last of which may now exist in full force; *but without the aid of Segeneration it will by no means account for the divergent evolution of any one of these species into a family of coexisting species.*

As I have just shown, Natural Selection is the exclusive generation of those better fitted to the environment; and it tends to the modification of species simply through the generation of the better fitted forms, while they are prevented from crossing with the less fitted, which fail of propagating through their lack of fitness. Now from the very nature of this process, which results from the success and failure of individuals in appropriating the resources of the environment, it follows that it cannot be the cause of separation between the successful competitors, and therefore any divergence of character that arises between the different groups of the successful cannot be attributed to Natural Selection. Natural Selection explains the prevention of crossing between the fitted and the unfitted, and shows how the successive generations of a species may gradually depart from the original type, becoming in time a different species; but *it cannot explain the divergences that arise between those that have, by the fact of successful propagation, proved their fitness.* It depends on superiority of adaptation to the environment, and tends to produce increasing adaptation; but *divergent kinds of adaptation are not necessary conditions for it, and it cannot be the cause of increasing divergence between the incipient kinds that otherwise arise.*

Divergent Evolution not explained by "the advantage of divergence of character."

Two sections of the 4th chapter of the 'Origin of Species' are given to the discussion of the "principle of benefit being derived from divergence of character," which it is maintained

"will generally lead to the most different or divergent variations being preserved and accumulated by natural selection." Now it cannot be doubted that ability to appropriate unused resources would be an advantage to any members of a community pressed for food; but I do not see how the divergence that would enable them to appropriate, for example, a new kind of food can be accumulated while free crossing continues; and Natural Selection cannot prevent the free crossing of competitors who leave progeny.

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 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 of 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.*

Natural Selection with Great Difference in External Conditions not sufficient to explain Divergent Evolution.

The insufficiency of Natural Selection without Segeneration to account for divergent evolution in an area where the external conditions are nearly uniform may be admitted by some who will claim that the case is quite otherwise when a species ranges freely over an area in which it is subjected to strongly contrasted conditions. It may be claimed that Diversity of Natural Selection resulting from a great difference in external nature is sufficient to account for divergent evolution without any Segeneration.

In the discussion of this subject, important light can be gained by referring to the experience of the breeder. This experience, in as far as it relates to the subject of Separation in the production of divergent breeds, may be arranged under three heads. 1st. Diversity of Selection without Separation. 2nd. Separation without Diversity of Selection. 3rd. Separation more or less complete with Diversity of Selection.

As the full discussion of these points is impossible here, and as there is probably but little difference of opinion in regard to what the results would be, I shall content myself with a simple statement of what I believe the experience of breeders shows. Difference in the standards of Selection without Separation can avail nothing in creating divergence of types; while Separation without difference in the standards of Selection will avail something, though food and external conditions are kept the same; but to secure the greatest divergence, in a given time, there must be both Diversity of Selection and complete Separation. In the case of Separation without Diversity of Selection there is room for difference of opinion; for the examples that some would claim as proving that there is often divergence without Diversity of Selection and without difference in external conditions may be attributed by others to unconscious Selection. It is granted by everyone that no skill in selecting the animals that possess the desired qualities will have any effect in establishing a new breed,

unless the selected animals are prevented from breeding with others that are deficient in the desired qualities. We further find that while Separation is an absolutely essential condition for this divergence, Diversity of Selection is not so essential. This is illustrated in the case of the slightly different types that are presented by the wild cattle found in the different parks of England,* a phenomenon which can hardly be attributed to any diversity in the environment.

In artificial breeding universal experience teaches that Variation and Selection, without Separation, do not produce divergence of races. The separate breeding of different classes of variation is a necessary condition for the accumulation of divergent variation; and wherever the separate breeding of different classes of variation is secured, there divergence of character is the result. In other words, Segregate Breeding is necessary to divergent evolution in gamogenetic animals.† Moreover, we have every reason to believe that the same law holds good throughout the whole organic world. The generating together of similars, with the exclusion or separation of dissimilars, is the central necessity in all evolution by descent, whether monotypic or polytypic; and *whatever causes the separate generation of different classes of variation will be the cause of divergent evolution.* That is, wherever this condition is added to the permanent laws of organic life, there divergence will follow. As we have already seen, Natural Selection or the Survival of the Fittest necessarily separates between the survivors and the non-survivors, between the best fitted and the least fitted, and is, therefore, the cause of monotypic transformation; but it cannot be the cause of separation between the different families of those that survive, and, therefore, cannot be the cause of divergence of character between these families. But we find that divergence of character often arises between the branches of one stock, and in many cases this divergence increases till well-marked varieties are established. If, therefore, the general principle we have just stated is true, there must be certain causes producing the

* See Darwin's 'Variation under Domestication,' chapter xv. 2nd page.

† In a subsequent paper I shall show how it is that Separate Breeding, long continued, inevitably ends in Segregate Breeding. In this chapter I confine my attention more especially to Separate Breeding when combined with Diversity of Selection in the different sections, for it is evident that this will produce Segregate Breeding.

Independent Generation of these forms; and, if we can discover these causes and trace them to general principles, they will, in connection with the laws of Variation and Selection, explain divergent evolution, that is the transformation of one form into many forms, of one species into many species. As community of evolution arises where there is community of breeding between those that through superior fitness have opportunity to propagate, so I believe it will be found that divergent evolution arises where there is separate breeding of the different classes of the successful. In other words, Exclusive Breeding of other than average forms causes Monotypic Evolution, and Segregate Breeding causes Divergent or Polytypic Evolution.

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 mollusks on the Sandwich Islands presents a great body of facts of this kind.

SELECTION OF EVERY KIND INSUFFICIENT TO ACCOUNT FOR DIVERGENT EVOLUTION.

Though I have no reason to doubt the importance of Sexual Selection in promoting the transformation of many species, I think I can show that unless combined with some separative or segregative influence, that prevents free intercrossing, it can avail nothing in producing a diversity of races from one stock. In the nature of its action Sexual Selection is simply exclusive. It is the exclusive breeding of those better fitted to the sexual instincts of the species, resulting from the failure to breed of the less fitted. It therefore indicates a method of separation between the better fitted and the less fitted; but it gives no explanation of separation between those that are equally successful in propagating.

I maintain that in a great number of animal species there are sexual and social instincts that prevent the free crossing of clearly marked races; but as these segregative instincts are rarely the cause of failure to propagate, and since when they are the cause of failure the failure is as likely to fall on one kind as on another, I conclude that the Segregate Breeding resulting from these instincts cannot be classed as either Sexual or Social Selection. Reflexive Selection in all its forms is, like Natural Selection, the result of success and failure in vital processes through which the successful propagate without crossing with the unsuccessful; but it in no way secures the breeding in separate groups of those that are successful in propagating. The exclusion of certain competitors from breeding is a very different process from the separation of the successful competitors into different groups that are prevented from intercrossing, and whose competition even is often limited to the members of the same group. Sexual Selection, like other forms of Reflexive Selection, can extend only as far as members of the same species act on each other. If the individuals of two groups have through difference in their tastes ceased to compete with each other in seeking mates, they are already subject to different and divergent forms of Sexual Selection; and is there any reason to attribute this difference in their tastes to the fact that, when there was but one group and the tastes of all were conformed to a single standard, some of the competitors failed of propagating, through being crowded aside by those more successful? *If the*

failure of the unsuccessful cannot be the cause of separation between the different kinds of the successful, then Selection, whether Natural, or Reflexive, or of any other kind, cannot be the cause of Divergent Evolution, except as co-operating with some cause of Independent Generation.

The failure of Sexual Selection, without Separation or Segregation, to account for divergent evolution, will perhaps be made clearer to some minds by considering some of the particular conditions under which it occurs. Suppose, for instance, that in some species of humming-bird there occurs a slight variation in the form or colour of the tail-feathers of the male that adds to the beauty of the individuals possessing the new character and rendering them more attractive to the females. We can see that they might have an advantage over their rivals in leaving progeny, and that the variety might in that way gradually gain the ascendency, and the beauty of the markings become more and more completely defined; but under such conditions what could prevent the whole species from being gradually transformed? Unless there was some separative or segregative principle that prevented the new variety from crossing with the others, the species would remain but one, though changed in some of its characters. We should have transformation without divergence.

The same must be true of Institutional Selection. It may be the cause of transformation; but it cannot be the cause of divergent evolution, unless there are added to it other causes that produce divergence in the character of the forms selected, and the separate breeding of the different groups of forms thus selected. A single illustration will set in a clear light the limitation in the influence of Institutional as well as all other Selection. In primitive communities the deaf are but little cared for, and owing to the great disadvantages of their position their opportunities for gaining subsistence, and therefore for rearing families, are greatly diminished: this is Natural Selection. Again, those who are at so great a disadvantage in communicating with their companions will be also at a disadvantage in finding consorts: this we may call Social Selection. Again, a community might either by law or by strict custom prevent the marriage of the deaf: this would be Institutional Selection. Any one of these forms of selection might be pressed so far as to be the means of increasing the average power of hearing in the community in succeeding generations; but it could never be the cause of two divergent

races, one with good powers of hearing and the other with an increasing liability to deafness. To secure such divergence it is necessary that segregative influences should be introduced, such as have been most amply furnished by the modern system of education for the deaf. Under these influences those endowed with hearing and those without hearing have been separated into two communities, the members of each having but little opportunity for acquaintance beyond the limits of that community; each community having separate schools, separate newspapers, and to some extent a separate language. As the result of this segregation marriages between the two classes have been greatly diminished; and little by little two races are arising, the hearing race and the deaf race.*

Reasons of a General Character for considering Selection without Independent Generation an Unsatisfactory Explanation of Divergent Evolution.

1. The divergence is often confined to characters which seem to have no possible relations of adaptation either to the environment or to other members of the species, and, therefore, to be independent of both Natural and Reflexive Selection.

2. Divergence relating to adaptive characters successfully propagated involves different kinds rather than different degrees of adaptation and advantage; and, as Adaptational Selection depends on the difference of degrees of advantage, it cannot account for the divergence of forms possessing equal degrees of advantage.

3. In the very nature of its action, we see that Adaptational Selection unaccompanied by Independent Generation must produce essentially *monotypic transformation*.

4. In artificial breeding, Independent Generation is found to be an essential condition for the production of divergent races; and there is no reason to doubt that the same law holds good in the divergence of natural forms.

5. The general fact that species possessing high powers and large opportunities for migration occupy large areas, while those

* See paper by Alexander Graham Bell, read before the National Academy of Sciences, November 13, 1883, upon the "Formation of a Deaf Variety of the Human Race;" also a review of the same in 'The Popular Science Monthly,' vol. xxvii. p. 15, entitled "Can Man be Modified by Selection?"

possessing low powers and small opportunities for migration divide the same area, or an area no larger, between many representative species, shows that independent generation is an important element in their divergence.

CHAPTER II.

Cumulative Divergence through Cumulative Segregation.

Local separation in dissimilar environments is the only cause of Segregation that has been clearly pointed out by Darwin. I shall, however, endeavour to show that there are other causes producing Segregation, and that, without any Change of Environment or change in the Environment, they may produce all the phenomena of Divergent Evolution. Any cause that, out of two or more kinds of successful variations, brings together one kind in such a way as to facilitate their breeding together, or to hinder their breeding with those of other kinds, is according to my definition a cause of Segregate Breeding; and the experience of breeders shows that wherever such causes operate divergent evolution is the result, and that the divergence accumulates when the process is continued through many generations. From their experiments we learn that any form of Segregate Breeding persistently continued will result in divergent evolution. As any form of natural selection in which other than typical forms have the advantage will result in Monotypic Evolution, so any form of segregate generation will produce Polytypic Evolution. I call this the law of *Cumulative Divergence through Cumulative Segregation.* It is a generalization established by the widest experience of mankind in the cultivation of plants and the breeding of animals; and any assumption that is not in accord with it may be wisely called in question.

I, therefore, judge that the advantage or disadvantage of their divergence, to individuals diverging from the typical form of a species, cannot be the factor that determines whether the divergence shall be accumulated.

A divergent member of any intergenerating group cannot long perpetuate its kind, if the divergence is any disadvantage; for the superior propagation of the more successful kinds will soon overpower the influence of the less successful; and the result will be Monotypic Evolution. The case is, however, very different with variations that are wholly or partially separated from

each other and from the type by their divergent adaptation to different kinds of resources, or by any other cause. The perpetuation of such variations depends not upon any advantage they possess above the type from which they diverge, but upon ability to appropriate from the environment sufficient simply to maintain existence, and the result is Polytypic Evolution. In other words, of the freely crossing forms of any species it is only those that are most successful that are perpetuated; while *of forms that are neither competing nor crossing, every kind is perpetuated that is not fatally deficient in its adaptations.* It follows that a form that under present conditions maintains only a precarious existence may, if kept from crossing, maintain its characteristics unimpaired for many generations, and at last, through changes in the environment, enter upon a period of great prosperity. Such would be the case with a form depending upon resources at first scarce, and afterwards very abundant.

Again, the individuals of a species that are brought together in their attempts to appropriate some new kind of resource, and are thus led to breed with each other, and not with the rest of the species, become a new Intergenerating Group in which a new and divergent form of natural selection is established, depending on divergent adaptations in the organism, without any change in the environment. The gradual process of gaining full adaptation to the new resources may extend over many generations, and during this long period the divergent form may be at a great disadvantage as compared with the typical form; but after this long process of divergence is completed, and full command of the new resource is gained, the new race may enter upon a period of great prosperity. In such a case, the period of most rapidly accumulating divergence is a period when the incipient race is suffering the heaviest disadvantage. The transformation from a wild to a domestic state affords a complete parallel to this process. In the initial and earlier stages, the divergent branch that is being domesticated is in constant danger of extermination; and it is only when a good degree of adaptation to the new conditions has been gained that it can be said to be as prosperous as the wild stock from which it was derived. Darwin has not explained how disadvantageous sexual instincts can be formed; but, assuming that there are such instincts, he has shown that they would modify the species in a way that is disadvantageous. He believes

the progenitors of man were deprived of their hairy coat by Sexual Selection that was, in its earlier stages, disadvantageous.

It is therefore evident that the simple fact of divergence in any case is not a sufficient ground for assuming that the divergent form has an advantage over the type from which it diverges. We may, however, be sure that there is some cause or combination of causes that facilitates the intergenerating of those similarly endowed, and hinders their crossing with other kinds; and if we can discover the cause of this Segregate Generation, we shall have an explanation of one part of the process by which the forms thus endowed are becoming a distinct race.

Separation and Segregation with the Principle of Intension.

It will contribute to clearness in our discussion if we can gain definite conceptions of the conditions that are necessarily involved in Separate and Segregate Breeding.

Separate Generation, which for convenience I call Separation, implies :—

1st. The indiscriminate separation of the members of a species into different sections that are prevented from freely crossing with each other.

2nd. The aggregation of the members of one section; that is, their being brought into conditions of time and place that allow of their freely crossing.

3rd. The integration of the members of each section into one intergenerating group, through the operation of functional adaptations by which the members of each section freely cross with each other. This analysis of the process shows that it may depend upon a great variety of causes, working together in a very complex way. We shall hereafter find that the causes of separation may operate in such a way that no aggregation or propagation takes place amongst the members that are separated from the old stock; but in such cases there is no Separate Generation, and therefore no Separation in the sense in which I use the word.

Segregate Generation also consists of separation, aggregation, and integration; but it differs from Separate Generation in that in the latter the separation is indiscriminate, while in the former there is a more or less pronounced bringing together of those that are similarly endowed, with separation of those that are

dissimilar. Segregate Generation is therefore the separation of dissimilars, with the aggregation and integration of similars. As we have already seen, Segregate Breeding may be produced by Separate Breeding accompanied by Diversity of Natural Selection in the different sections. It is also evident that any other cause that develops in one or more of the separate sections of the species characters that are not found in the other sections will produce Segregate Breeding. Such cases are Diversity of Selection of other forms than Natural Selection, Diversity in the inherited effects of Use and Disuse (unless physiologists have been mistaken in supposing that there are any such effects), and Diversity in the inherited characters derived from the Direct Effects of the Environment (unless, again, Weismann is right and the general belief wrong). Segregate Breeding may, moreover, be produced directly by the very way in which the separation of the different sections is secured. One of the best examples of this kind of Segregation is seen in what I call Industrial Segregation, where the members of a species are distributed according to their endowments, those of similar endowments being brought together. In such cases, Segregation is introduced as soon as the Separation, without depending on the subsequent action of the environment, or on diverse forms of Use, or of Selection; though there can be no doubt that, in the great majority of cases, Diversity of Use and Diversity of Selection of some kind will in time come in to intensify the result.

There is another invariable sequence which it is necessary we should keep in mind, if we would understand the relation in which these two principles stand to each other. I refer to the certainty that all prolonged Separate Breeding will be transformed into Segregate Breeding. In other words, indiscriminate separation, in which there is no apparent difference in the different groups, is in time found to be a separation in which there is a decided difference in the different groups. Whenever a sufficient number of the same species to ensure propagation are brought together in an isolated position, Separate Generation is the result; and, if this Separate Generation is long-continued, we have reason to believe, it always passes into Segregate Generation with divergent evolution. The fundamental cause for this seems to lie in the fact that no two portions of a species possess exactly the same average character, and that the initial differences are for ever reacting on the environment and on each other in

such a way as to ensure increasing divergence in each successive generation, as long as the individuals of the two groups are kept from intergenerating. In my paper on *Diversity of Evolution under one Set of External Conditions*, I spoke of this principle of divergence as "Separation with Variation;" but in order to distinguish the antecedent condition, which is Separation, from the result, which is something more than Variation, I now call the certainty that some form of divergent transformation will arise when intergeneration is prevented the principle of *Intension*; and Segregation produced by independent transformation I call Intensive Segregation.

As Separate and Segregate Generation are so closely related, I have, in order to avoid a multiplication of terms, classified the two principles together under the general term Segregation. In my discussion of the causes of Segregation I shall, however, endeavour to determine concerning each class of causes whether they are primarily Separative or Segregative.

A full discussion of the causes of Segregation would require that under each combination of causes to which we give a distinctive name we should show:—

1. How the Independent Generation is produced.
2. How the difference of character in the different sections is produced.
3. How the aggregation in place bringing together the members of each section is produced.
4. How the correspondence in times and seasons necessary for intergeneration is secured within each section.
5. How the correspondence of community and of Sexual and Social instincts necessary for intergeneration is secured within each section.
6. How the correspondence in structure, in dimensions, and in the mutual potentiality of the sexual elements necessary for intergeneration is secured within each section.

It will, however, be observed that, with the exception of the two first, these questions relate to the necessary conditions that must always exist in the case of every intergenerating group; and as it is evident that intergeneration in some degree must be the normal condition in every sexual, that is in every gamogenetic, species, we may here assume that all the conditions necessary to intergeneration exist, except so far as they have been disturbed by causes producing Segeneration. In tracing

the causes of Segregation it will therefore be sufficient if in each class of cases we give the cause of Segeneration, showing why the same cause does not prevent all intergeneration, and explain the difference of character in the different sections produced by the Segeneration. In full accord with the implications of the theory of evolution, we proceed on the assumption that intergeneration was the original condition of every species, and that the intergeneration of those that are brought together under favourable circumstances may be taken for granted, unless there is some special cause that prevents. All that is necessary to produce Separation is the failure of any one of the many conditions on which free-crossing depends, in such a way, and to such a degree, that the species falls into two or more sections between which crossing is interrupted, without its being interrupted within the bounds of each section. And all that is necessary to produce Segregation is that to Separation should be added some cause that secures difference of character in the different sections. And as Separation long continued inevitably ends in Segregation through the development of difference of character in the different sections, we need not in our classification set them wholly apart, though for the sake of clearly recognizing the difference it will be well to note in each class of causes whether the primary effect is Separation or Segregation.

Cumulative Segregation and the Classification of its Different Forms.

The fundamental law to which I would call attention may be expressed in the following formula:—Cumulative Segregation produces accumulated divergence; and accumulated divergence produces permanent Segregation; and the Segregate subdivision of those permanently Segregated produces the divisions and subdivisions of organic phyla. If, then, we can discover the causes of Segregation, we shall understand the causes of a wide range of phenomena; for this is the fundamental principle in the formation of varieties, species, genera, families, orders, and all greater divergences that have been produced in the descendants of common ancestry.

In treating of the causes of Segregation, I have found it convenient to make two distinct classifications. In the one the

fundamental distinction is between segregation produced by the purpose of man, which I call

RATIONAL SEGREGATION, in its two forms:

ARTIFICIAL SEGREGATION,
INSTITUTIONAL SEGREGATION,

and that produced by nature outside of man, which I call

RESPONSIVE SEGREGATION;

while any of these forms of Segregation may be intensified by Independent transformation through the principles of Diversity of Selection, Diversity of Use, or Diversity of Direct Effects of the Environment; and the combined action of Segregation with these and other principles of transformation I call

INTENSIVE SEGREGATION.

In the other classification, the fundamental distinction is between segregation arising from the relations in which the organism stands to the environment, which I call

Environal Segregation,

and segregation arising from the relations in which the members of the same species stand to each other, which I call

Reflexive Segregation;

while any form of segregation belonging to either of these classes may be enhanced by one or more of the forms of Intension, and thus present what I call

Intensive Segregation.

THE EFFECTS OF SEGREGATION.

The effects of Segregation can be studied to advantage in the vast experience that has been accumulated in the domestication of plants and animals.

Artificial Segregation is caused by the relations in which the organism stands to the rational environment, that is to the purposes of man. In other words, Artificial Segregation is the rational form of Environal Segregation. Though the bearing of Segregation on the evolution of species in a state of nature has been for the most part overlooked, its effects have been quite familiar to the breeder of domestic races.

As a convenient method of illustration, let us consider the different results that will be gained according as we subject the same ten pairs of wild rock-pigeons to one or the other of the following methods of treatment.

In the first experiment let the treatment be as follows:—Let ten aviaries be prepared; and in each aviary put one male with the female that most nearly resembles it. When the young of each aviary arrive at maturity, let them be inspected, and if any individual resembles the inmates of one of the other aviaries more than the inmates of the aviary in which it was produced, let it be placed with those it most closely resembles. If any unusual variation arises, let it be placed in a new aviary, and let the one of the other sex that most closely resembles it in that respect be placed with it. When the crowding in any aviary becomes injurious to the health of the birds let the numbers be indiscriminately reduced. Let this process be continued many generations, the inmates in all the aviaries being fed on the same food, and in every respect treated alike, and what will be the result?

No experienced breeder will hesitate in assuring us that under such treatment a multitude of varieties will be formed, many of which will be very widely divergent from the original wild stock. In other words, *Cumulative Segregation will produce accumulated divergence, though there is no Selection in the sense in which Natural Selection is Selection.*

Again, let us take the same ten pairs, and putting them into one large aviary, let them breed freely together without any Segregative influence coming in to affect the result; and who does not know that the type would remain essentially one though a considerable range of individual variation might arise. That is, *without Segregation no divergence of type will arise.*

The Natural Law of Cumulative Segregation.

I shall now show that there is in nature a law of Cumulative Segregation. There are large classes of activities in the organism and in the environment that conspire to produce Segregate Breeding; and to produce it in such a way that, in a vast multitude of cases, it becomes a permanent fact, which no cause that we are acquainted with can ever obliterate. Moreover, when one form of Segregation has become fully established, we

find that the different branches are liable to be again subjected to segregative influences, by which each branch is subdivided, and in time differentiated into divergent forms that are not liable to intercross in a state of nature.

Now, as we have just pointed out, we know, from the fundamental laws of the organic world, that Cumulative Segregation of this kind must produce Cumulative Divergence of Types.

The Segregation that results from the natural causes enumerated in this paper is cumulative in two respects. In the first place, every new form of segregation that now appears depends on, and is superimposed upon, forms of Segregation that have been previously induced; for when Negative Segregation arises, and the varieties of a species become less and less fertile with each other, the complete infertility that has existed between them and some other species does not disappear, nor does the Positive Segregation (that is, the prevention of the consorting of the species characterized by this mutual incapacity) cease. The means by which the males and females of one species find each other are not abrogated when the species falls into segregated varieties. 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.

The principle of Cumulative Segregation, first in its independent action, and still further when combined with the different principles by which the divergence of the segregated branches is intensified, gives a formal explanation of the ever-expanding diversities of the organic world. It shows how varieties arise and pass into species, how species pass into genera, genera into families, families into orders, and orders into classes and the higher divisions, as far as evolution by descent extends. It brings to light the dependence of this whole process on the influences that produce segregation; and shows how these influences, added to Variation, Heredity, and the other acknowledged powers residing in organisms, must produce the phenomena of divergent evolution.

Competitive Disruption.

Before entering upon the discussion of the direct causes of Cumulative Segregation, let us briefly consider a law resulting from the competition of kindred with each other, which brings to light the fact that such competition is one of the most important factors in preparing the way for, and in giving intensity to, the activities that lead to Segregation and divergent evolution. It is manifest that competition for identical resources and Geographical Segregation are conditions which cannot exist at the same time between the same members of any species; but it is also manifest that, when there are no natural barriers separating the different districts of an area part of which is occupied by a species, pressure for food through a great increase in the population will tend to distribute the species over the whole area; and, if the available resources in the different districts are considerably diverse, the overflow of population from the crowded district will be subjected to a necessary change of habits; and thus, through competition, there will be the disruption of old relations to the environment, and the bringing in of conditions that give the highest efficiency and the fullest opportunity to all the activities that produce Segregation. In the case of animals, no condition can tend more strongly to produce migration than scarcity of food in the old habitat; and in the case of both plants and animals, a great increase in the numbers that are exposed to the winds, currents, and other transporting influences of the environment increases the probability that individuals will be carried to new districts where circumstances will allow of their multiplying, and where they will, at the same time, be prevented from crossing with the original stock. In many cases the segregation thus brought about will be in districts where the environment is the same, and in other cases the pressure for food or other resources will lead portions of the species to take up new habits in the effort to appropriate resources not previously used; and through these new habits they will often be segregated from those maintaining the original habits. I shall hereafter show that in both these cases there is a tendency to divergent evolution.

I at one time thought of describing this principle as a form of Segregation, calling it *dominational segregation*; but fuller reflection convinces me that the domination of the strong over

the weak is not a form of Segregation, but rather a cause that prepares the way for Segregation, by forcing portions of the community out of their inherited relations to the environment.

CHAPTER III.

Description and Classification of the Causes of Cumulative Segregation.*

A. Environal Segregation.

Environal Segregation is Segregation arising from the relations in which the organism stands to the environment.

It includes four classes, which I call Industrial, Chronal, Spatial, and Artificial Segregation.†

(*a*) Industrial Segregation

is Segregation arising from the activities by which the organism protects itself against adverse influences in the environment, or by which it finds and appropriates special resources in the environment.

The different forms of Industrial Segregation are Sustentational, Protectional, and Nidificational Segregation.

For the production of Industrial Segregation it is necessary that there should be, in the same environment, a diversity of fully and of approximately available resources more or less separated from each other, and in the organism some diversity of adaptation to these resources, accompanied by powers of search and of discrimination, by which it is able to find the resources for which it is best fitted and to adhere to the same when found.

The relation in which these causes stand to each other and through which they produce segregation may be described as separation according to endowment produced by endeavour according to endowment.

It is evident that if initial variation presents in any case a diversity of adaptations to surrounding resources that cannot be

* In the following chapters numerals are attached to what I consider separate causes of segregation independent of human purpose.

† Francis Galton has suggested another class, which might appropriately be called Fertilizational Segregation.

followed without separating those differently endowed, we shall have, in the very nature of such variation, a cause of segregation and of divergent evolution. Some slight variation in the digestive powers of a few individuals makes it possible for them to live exclusively on some abundant form of food, which the species has heretofore only occasionally tasted. In the pressure for food that arises in a crowded community these take up their permanent abode where the new form of food is most accessible, and thus separate themselves from the original form of the species. These similarly endowed forms will therefore breed together, and the offspring will, according to the law of Divergence through Segregation, be still better adapted to the new form of food. And this increasing adaptation, with increasing divergence, might continue for many generations, though every individual should come to maturity and propagate; that is, though there were no enhancing of the effect through Diversity of Selection, or indeed through any other cause producing Intensive Segregation. And when different forms of Intension do arise, they may be entirely independent of change in the environment, the only change being in the forms or functions of the organism.

In choosing a name for this form of Segregation I first thought of calling it Physiological or Functional Segregation. But such a name is, on closer examination, found to imply both too much and too little; for on the one hand there is probably no form of segregation that is not in some way or in some degree due to physiological or functional causes, and on the other hand this special form of segregation is as dependent on psychological causes which guide the organism in finding and in adhering to the situation for which it is best fitted, as it is on the initial divergence of the more strictly physiological adaptations by which it is able to appropriate and assimilate the peculiar form of resource. In the case of freely moving animals, the psychological guidance is an essential factor in the success of the individual; while in the case of plants and low types of animal life, the suitable situation is reached by a wide distribution of a vast number of seeds, spores, or germs, and the same situation is maintained by a loss of migrational power as soon as the germs begin to develop. In these lower organisms it is evident that the success of the individual must depend on its physiological rather than on its psychological adaptations; and if an initial divergence of adaptations results in a slight difference in the kinds

that succeed in germinating in contrasted situations, the difference is directly due to a Diversity in the forms of Natural Selection affecting the seed, and the Separation is what I hereafter describe as Local Separation passing into Local Segregation. We therefore see that what I here call Industrial Segregation depends on psychological powers acting in aid of divergent physiological adaptations to the environment, or in aid of adaptations that are put to different uses.

Observation shows that there is a multitude of cases in which Endeavour according to Endowment brings together those similarly endowed and causes them to breed together; and when the species is thus divided into two or more groups somewhat differently endowed, there will certainly be an increased divergence in the offspring of the parents thus Segregated; and so on in each successive generation, as long as the individuals find their places according to their endowments, and thus propagate with those similarly endowed, there will be accumulated divergence in the next generation. Indeed it is evident that Endeavour according to Endowment may produce under one environment what Natural Selection produces when aided by local separation in different environments. As it produces the separate breeding of a divergent form without involving the destruction of contrasted forms, it is often the direct cause of divergent transformations; while Natural Selection, which results in the separate breeding of the fitted through the failure of the unfitted, can never be the cause of divergence, unless there are concurrent causes that produce both divergent forms of Natural Selection, and the separate breeding of the different kinds of variations thus selected.

Suetudinal Intension.—Another law is usually believed to be connected with Endeavour which, if it exists, must conspire to enhance its tendency to produce divergent evolution. I refer to the influence which the habitual endeavour of the parents has on the inherited powers of the offspring. We may call it the law of Endowment of Offspring according to the Exercise or Endeavour of Parents, or more briefly Suetudinal Intension. The inherited effects of use and disuse have been fully recognized by Darwin, Spencer, Cope, Murphy, and others, and need not here be discussed. The one point to which I wish to call attention is, that in order that diversity of use should produce divergent evolution, it is necessary that free crossing should be prevented between the different sections of the species in which the

diversity of use is found. Now this condition of separate breeding is often secured by Industrial Segregation. In other words, the law of Endeavour according to Endowment, often secures Separation according to endowment; and this gives an opportunity for the inheritable effects of diversity of endeavour to be accumulated in successive generations; and in this way both laws conspire to produce divergent evolution.

In the relation of these two factors we have a striking example of the peculiar interdependence of vital phenomena. Diversity of endowment is the cause of diversity of endeavour and of Segregate Breeding, and diversity of endeavour with Segregate Breeding is the cause of increased diversity of endowment. It is very similar to the relation between power and exercise in the individual. Without power there can be no exercise, and without exercise there can be no continuance or growth of power.

We, therefore, see that the effects of Industrial Segregation are specially liable to be enhanced by that form of Intensive Segregation which I have suggested should be called Suetudinal Intension.

Simple and familiar as the principles of Industrial Segregation and Suetudinal Intension may seem, their consistent application to the theory of evolution will throw new light on a wide range of problems. This law of divergent evolution through Industrial Segregation rests on facts that are so fully acknowledged by all parties, that it seems to be a superfluous work to gather evidence on the subject. It may, however, be profitable to consider briefly whether the cases are frequent in which different habits of feeding, of defence, or of nest-building become the cause of separate breeding by which the same habits are maintained in one line of descent without serious interruption for many generations. It is important to remember, (1) that the separate breeding will arise with equal certainty whether the diversity in the habits has been initiated by original diversity in the instincts and adaptations of the different variations, or by the crowding of population inducing special efforts to find new resources, and leading to diversity of endeavour; and (2) that in either case the result is what is here called Industrial Segregation. In the first case the process is directly Segregative, while in the second case it is primarily Separative, but (according to the principle discussed in the second section of last chapter) inevitably passes into Segregate Breeding. Suetudinal Intension, or Divergent

Evolution through Diversity of Use, will operate as surely in the one case as in the other.

1. *Sustentational Segregation* arises from the use of different methods of obtaining sustentation by members of the same species.

There can be no doubt that of the innumerable cases where phytophagic varieties (as they are sometimes called) of insects exist, a considerable proportion would be found on investigation to be permanent varieties producing offspring that are better adapted to the use of the special form of food consumed by the parents than are the offspring of other varieties; and it is evident that if the peculiar habits of each variety had no tendency to produce segregative breeding this result would not be reached; for each variety would be promiscuously mingled with every other, and, though the tendency to variation might be greatly increased, the regular production of any one variety of young would be prevented.

A large mass of facts could be easily gathered illustrative of Sustentational Segregation; but as the principle will probably be denied by no one, we shall pass on without further expansion of this part of the subject.

2. *Protectional Segregation* is Segregation from the use of different methods of protection against adverse influences in the environment.

When a new enemy enters the field occupied by any species different methods of escape or defence are often open to the members of the one species; and the use of these different methods must sometimes result in the segregation of the members according to the methods adopted. Some may hide in thickets or holes, while others preserve themselves by flight. Supposing the species to be an edible butterfly occupying the open fields, and the new enemy to be an insectivorous bird also keeping to the open country, certain members might escape by taking to the wood-lands, while others might remain in their old haunt, gaining through Protectional Selection more and more likeness to some inedible species.

3. *Nidificational Segregation.*—Let us now consider the effects of divergent habits in regard to nest-building. It is well known to American ornithologists that the Cliff Swallow of the eastern portions of the United States has for the most part ceased to build nests in the cliffs that were the original haunts of the

species, and has availed itself of the protection from the weather offered by the eaves of civilized houses; and that with this change in nest-building has come a change in some of its other habits. Now there is reason to believe that if the number of houses had been limited to a hundredth part of those now existing, and if that limited number had been very slowly supplied, this gradual change in some of the elements of the environment would have resulted in divergent forms of adaptation to the environment in two sections of the same species. One section would have retained the old habit of building in the cliffs, with all the old adaptations to the circumstances that depend on that habit; while another section of the species would have availed itself of the new opportunities for shelter under the eaves of houses, and would have changed their inherited adaptations to meet the new habits of nest-building and of feeding. It is also evident that the prevention of free interbreeding between the different sections caused by the diversity of habits would have been an essential factor in the divergence of character in the sections.

It simply remains to consider whether the industrial habit that separates an individual from the mass of the species will necessarily leave it alone, without any chance of finding a consort that may join in producing a new intergenerant. The answer is that there is no such necessity. Though it may sometimes happen that an individual may be separated from all companions by its industrial habit, it is usually found that those that at one time and one place adopt the habit are usually sufficient to keep up the new strain, if they succeed in securing the needed sustenance.

(*b*) Chronal Segregation

is Segregation arising from the relations in which the organism stands to times and seasons.

I distinguish two forms—Cyclical and Seasonal Segregation.

4. *Cyclical Segregation* is Segregation arising from the fact that the life cycles of the different sections of the species do not mature in the same years.

A fine illustration of this form of Segregation is found in the case of *Cicada septemdecim*, whose metropolis is in Virginia, Maryland, and Delaware, though many out-lying broods are found in other regions east of the Mississippi River. The typical form has a life-cycle of seventeen years, but there is a special

race (*Cicada tredecim*, Riley) that is separated from the typical form, both locally and chronally. As the life-cycle of this race is thirteen instead of seventeen years, even if occupying the same districts and breeding at exactly the same season, interbreeding could occur between the two forms only once in 221 years, or once in 13 generations of the longer lived race, and once in 17 generations of the shorter lived race. During the year 1885 the two races appeared simultaneously. The opportunity for testing whether they would freely interbreed if brought together has, therefore, passed not to return till the year 2106; but the distribution of the two races in different districts seems to indicate that Local Segregation has had an important influence in the development of the race. It is manifest, however, that if during a period of local separation, or if during the period of 221 years of Cyclical separation after the thirteen-year race was first formed, this race should become modified in the season of its appearing, there would after that be no mingling of race, though brought together in the same districts. This would be Seasonal Segregation, which we shall consider in the next section; but what is of special interest here, as an example of complete Cyclical Segregation, is the fact that at Fall River, Massachusetts, there is a brood of the *septemdecim* form, due a year later than the universal time of appearing.*

In any species where the breeding of each successive generation is separated by an exact measure of time which is very rigidly regulated by the constitution of the species, Cyclical Segregation will follow, if, through some extraordinary combination of circumstances, members sufficient to propagate the species are either hastened or delayed in their development, and thus thrown out of synchronal compatibility with the rest of the species. If, after being retarded or hastened in development so that part of a cycle is lost or gained, the old constitutional time measure reasserts itself, the Segregation is complete.

So far as this one point relating to the time of maturing is concerned the constitutional difference is segregative, while in every other respect it will be simply separative, except as separation passes into Segregation. The Fall-River brood of *Cicada*

* See statement by Prof. C. V. Riley, in 'Science,' vol. vi. p. 4. For particulars concerning the distribution and habits of this species see a paper by Prof. Riley, read before the Biological Society of Washington, May 30, 1885, extracts from which are given in 'Science,' vol. v. p. 518.

septemdecim being entirely separated from all other broods of the same race by being belated a year, may be modified by forms of Natural Selection that never arise in these other broods. And this may be the case even if a brood observing the ordinary time is always associated with it in locality.

5. *Seasonal Segregation* is produced whenever the season for reproduction in any section of the species is such that it cannot interbreed with other sections of the species. It needs no argument to show that if, in a species of plant that regularly flowers in the Spring, there arises a variety that regularly flowers in the autumn, it will be prevented from interbreeding with the typical form. The question of chief interest is, under what circumstances are varieties of this kind likely to arise? Is a casual sport of this kind likely to transmit to subsequent generations a permanently changed constitution? If not, how is the new constitution acquired? One obvious answer is that it may arise under some special influence of the environment upon members of the species that are geographically or locally segregated from the rest of the species.

But may not the variation in the season of flowering be the cause of segregation that will directly tend to produce greater variation in that respect in the next generation, and so on till the divergence in the constitutional adaptation to season is carried to the greatest extreme that is compatible with the environment? I believe that it not only may, but must have that effect; but we should remember that the average form which flowers at the height of the season will so vastly predominate over the extreme forms that the latter will be but stragglers in comparison.

In regard to the one point of the season of readiness for propagation, this principle is segregative; but in other respects it is simply separative, unless through the principle of correlated variation other characters are directly connected with the constitution that determines the season. It will be observed that Seasonal Segregation is produced by a parallel and simultaneous change in the constitution of members in one place sufficient to propagate the species; while Cyclical Segregation is produced by a simultaneous acceleration or retardation in the development of members in one place sufficient to propagate the species without disturbing the regular action of the constitution under ordinary circumstances.

(*c*) Spatial Segregation

is Segregation arising from the relations in which the organism stands to space.

I distinguish two forms, viz. Geographical and Local Segregation.

Geographical Segregation is Segregation that arises from the distribution of the species in districts separated by geographical barriers that prevent free interbreeding. Decided differences of climate in neighbouring districts and regions may be classed as geographical barriers.

Local Segregation is Segregation that arises when a species with small powers of migration and small opportunities for transportation has been, in time, very widely distributed over an area that is not subdivided by geographical barriers. The Segregation in this case is due to the disproportion between the size of the area occupied and the powers of communication existing between the members of the species occupying the different parts of the area. Though it is often difficult to say whether a given case of Segregation should be classed as Geographical or Local, still the distinction will be found useful; for the results will differ according as the Segregation is chiefly due to barriers or to wide diffusion of the species. In Geographical Segregation the result is usually the development of well-defined varieties or species on opposite sides of the barriers; but in Local Segregation it often happens that the forms found in any given locality are connected with those in surrounding localities by individuals presenting every shade of intermediate character; and in general terms it may be said that the forms most widely separated in space are most widely divergent in character. It is of course apparent that when the divergence has reached a certain point the differentiated forms may occupy the same districts without interbreeding, for they will be kept apart by some, if not all, of the different forms of Industrial, Chronal, Conjunctional, and Impregnational Segregation.

Three different forms of Spatial Segregation may be distinguished according to the causes by which they are produced, viz.:—

6. *Migrational Segregation*, caused by powers of locomotion in the organism.

7. *Transportational Segregation*, caused by activities in the environment that distribute the organism in different districts, (prominent among these are currents of atmosphere and of

water, and the action of migratory species upon those that can simply cling).

8. *Geological Segregation*, caused by geological changes dividing the territory occupied by a species into two or more sections. For example, geological subsidence may divide the continuous area occupied by a species into several islands, separated by channels which the creatures in question cannot pass.

Migration differs from transportation simply in that the former is the direct result of activities in the organism, and the latter of activities in the environment; and though the distribution of every species depends on the combined action of both classes of activities, it is usually easy to determine to which class the carrying power belongs. The qualities of the thistle-down enable it to float in the air, but it is the wind that carries it afar.

Some degree of Local Segregation exists whenever the members of a species produced in a given area are more likely to interbreed with each other than with those produced in surrounding areas, or whenever extraordinary dispersal plants a colony beyond the range of ordinary dispersal. In other words, when those produced in a given district are more nearly related with each other than with those produced in surrounding districts, there local segregation has existed.

There is one important respect in which Spatial Segregation differs from all other forms of Environal Segregation, namely, in its ordinary operation it does not depend directly upon diversity in the qualities and powers of the organism. The dispersion of the members of a species would not be prevented if each was exactly like every other; though, of course, if there were no power of variation, separate breeding would have no influence in producing divergence of character. It follows that every species is, or is more or less liable to be, affected by Spatial Segregation; and it often happens that other forms of Segregation arise through the previous operation of this form; but as Spatial Segregation prevents organisms from crossing only when separated in space, it must always be reinforced by other forms of segregation before well-defined species are produced that are capable of occupying the same district without interbreeding. The vast majority of the divergent forms arising through Local Segregation are reintegrated with the surrounding forms, new divergences constantly coming in to take the place of the old;

but if, during its brief period of local divergence, Industrial or Chronal Segregation is introduced, the variety becomes more and more differentiated, and, as one after another the different forms of Reflexive Segregation arise, it passes into a well-defined species. There is, however, reason to believe that the order of events is often the reverse, Reflexive forms of Segregation being the cause of the first divergences.

As Spatial Segregation does not depend upon diversity in the qualities and powers of the organism, so also it does not usually result in distributing the organism in different localities according to their differences of endowment. The causes that produce it are primarily separative, not segregative.

Migration is produced by the natural powers of the organism, acting under the guidance of instincts that usually lead a group of individuals, capable of propagating the species, to migrate together; while the organisms that are most dependent on activities in the environment for their distribution, are usually distributed in the form of seeds or germs, any one of which is capable of developing into a complete community.

The causes of Separation between the different sections, and of Integration between the members of one section, are therefore sufficiently clear; but what are the causes of difference of character in the different sections, especially when they are exposed to the same environment? These causes all come under what I call Intensive Segregation, which, for the sake of saving repetition, will be fully discussed in a separate paper.

(*d*) 9. Fertilizational Segregation.

Since writing this chapter on Environal Segregation, I have seen Francis Galton's short article on "The Origin of Varieties" published in 'Nature,' vol. xxxiv. p. 395, in which he refers to a cause of segregation that had not occurred to me. He says:—"If insects visited promiscuously the flowers of a variety and those of the parent stock, then—supposing the organs of reproduction and the period of flowering to be alike in both, and that hybrids between them could be produced by artificial cross-fertilization—we should expect to find hybrids in abundance whenever members of the variety and those of the original stock occupied the same or closely contiguous districts. It is hard to account for our not doing so, except on the supposition that insects feel repugnance to visiting the plants interchangeably."

Following the form of nomenclature adopted in this paper, I venture to call this principle Fertilizational Segregation.

It is evident that Segregation of this form depends on divergence of character already clearly established, and therefore on some other form of Segregation that has preceded. It is also segregative rather than separative, in that it perpetuates a segregation previously produced, which might otherwise be obliterated by the distribution of the different forms in the same district. The form of Segregation that precedes Fertilizational Segregation, producing the conditions on which it depends, must, from the nature of the case, be Local Segregation. Chronal and Impregnational Segregation, when imperfectly established, might be fortified by Fertilizational Segregation; but, in the case of plants, these are all dependent on previous Local Segregation.

(*e*) Artificial Segregation.

Artificial Segregation is Segregation arising from the relations in which the organism stands to the rational environment. As the operation of this cause is familiar, and as it was considered in the last chapter when discussing the effects of segregation, we pass on, simply calling attention to the fact that it is a form of Environal Segregation.

The Importance of Environal Segregation.

We must not assume that the various forms of Environal Segregation are of small influence in the formation of species because Sexual or Impregnational Incompatibility is a more essential feature, without which all other distinctions are liable to be swept away. The importance of the forms of segregation discussed in this chapter lies in the fact that they often open the way for the entrance of the more fundamental forms of segregation, even if they are not essential conditions for the development of the same. Though myriads of divergent forms produced by Local and Industrial Segregations are swept away in the struggle for existence, and myriads are absorbed in the vast tides of crossing and intercrossing currents of life, the power of any species to produce more and more highly adapted variations, and to segregate them in groups that become specially adapted to special ends, or that grow into specific forms of beauty and internal harmony, is largely dependent on these factors.

CHAPTER IV.

Description and Classification of the Causes of Cumulative Segregation (*continued*).

B. Reflexive Segregation.

Reflexive Segregation is Segregation arising from the relations in which the members of one species stand to each other.

It includes three classes, which I call Conjunctional, Impregnational, and Institutional Segregation.

It is important to observe that Intergeneration requires compatibility in all the circle of relations in which the organism stands; but, in order to ensure Segeneration between any two or more sections of a species, it is sufficient that incompatibility should exist at but one point. If either sexual or social instincts do not accord, if structural or dimensional characters are not correlated, if the sexual elements are not mutually potential, or if fixed institutions hold groups apart, Intergeneration is prevented, and Segeneration is the result, either as Segregation, or as Separation that is gradually transformed into Segregation.

(*a*) Conjunctional Segregation.

Conjunctional Segregation is Segregation arising from the instincts by which organisms seek each other and hold together in more or less compact communities, or from the powers of growth and segmentation in connection with self-fertilization, through which similar results are gained.

I distinguish four forms—Social, Sexual, Germinal, and Floral Segregation.

10. *Social Segregation* is produced by the discriminative action of social instincts.

The law of social instinct is preference for that which is familiar in one's companions; and, as in most cases the greatest familiarity is gained with those that are near of kin, it tends to produce breeding within the clan, which is a form of Segregate Breeding. If the clan never grows beyond the powers of individual recognition, or if the numbers never become so great as to impede each other in gaining sustenance, there will be but little occasion for segregation; but multiplication will lead to segmentation. Wherever the members of a species, ranging freely

over a given area, divide up into separate herds, flocks, or swarms, of which the members produced in any one clan breed with each other more than with others, there we have Social Segregation.

It should always be kept in mind that Social Segregation arises at a very early stage, holding apart groups not at all or but very slightly differentiated; while in the case of many animals, the eager sexual instincts of the males constantly tend to break up these minor groups. Though the barriers raised by social insincts are often broken over, their influence is not wholly overcome; and in many intstances the Social Segregation becomes more and more pronounced, till in time decided Sexual Segregation comes in to secure and strengthen the divergence.

11. *Sexual Segregation* is produced by the discriminative action of sexual instincts.

There can be no doubt that sexual instincts often differ in such a way as to produce segregation. But how shall we account for these differences? In the case of Social Segregation there is no difficulty, for it seems to be, like migration, due to a constant instinct, always tending to segregation. We also see that an endowment which prevents the destruction of the species through the complete isolation of individuals, and which co-operates with migrational instincts in securing dispersal without extinction, may be perfected by the accumulating effects of its own action. And is there any greater difficulty in accounting for the law that regulates sexual instincts? If it can be shown that Vigour and Variation, the conditions on which adaptation depends, are in their turn dependent on some degree of crossing, there will be no difficulty in attributing the development of an instinct that secures the crossing to the superior success of the individuals that possess it in even a small degree. On the other hand, whenever there arises a variety that can maintain itself by crosses within the same variety, any variation of instinct that tends to segregation will be preserved by the segregation. It needs no experiments to prove that, if the members of a species are impelled to consort only with the members of other species, they will either fail to leave offspring, or their offspring will fail to inherit the characteristics of the species. The same is true concerning the continuance of a variety that is not otherwise segregated. The power of variation on the one hand, and the power of divergent accumulation of variations on the other hand, are prime necessities for creatures that are wresting a living from a

vast and complex environment; and the former is secured by the advantage over rivals possessed by the variations that favour crossing, and the latter by the better escape from the swamping effect, and sometimes from the competition of certain rivals, secured by the more segregative variations. We must therefore believe that, whenever in the history of an organism there arise segregative variations which are able to secure sufficient sustentation and propagation to continue the species, the segregative quality of the forms thus endowed will be preserved and accumulated through the self-accumulating effect of the segregative endowments.

It is probable that in many of the higher vertebrates sexual instincts tend to bring together those of somewhat divergent character, but the difference preferred is within very narrow limits; and beyond those limits, it may be said that the general law for sexual attraction is, that it varies inversely as the difference in the characters of the races represented, if not inversely as some power of such difference. The action of such a law is necessarily segregative, whenever the divergence has, through other causes, passed beyond the limit of higher attraction. Before Sexual Segregation can arise, there must arise distinctive characteristics by means of which the members of any section may discriminate between those of their own and other sections. If there are no constant characteristics, there can be no constant aversion between members of different groups, no constant preference of those of one's own group. From this it follows, that before Sexual Segregation can arise, some form of Segregation that is not dependent on accumulated divergence of character must have produced the divergence on which the Sexual Segregation depends. Such forms are Local, Social, and some kinds of Industrial Segregation. When varieties have arisen through these causes, it often happens that Sexual Segregation comes in and perpetuates the Segregation which the initial causes can no longer sustain. As long as the groups are held apart by divergent sexual instincts, it is evident that divergent forms of Sexual Selection are almost sure to arise, leading to a further accumulation of the divergence initiated by the previous causes.

If there is any persistent cause by which local and social groups are broken up and promiscuously intermingled before recognizable characters are gained, the entrance of Sexual Segregation will be prevented. I therefore conclude that the chief

influence of this latter factor is found in its prolonging and fortifying the separate breeding of varieties that have arisen under Local, Social, or Industrial Segregation, and in thus continuing the necessary condition for the development of increasingly divergent forms of Intensive Segregation, under which the organism passes by the laws of its own vital activity when dealing with a complex environment in groups that never cross.

12. *Germinal Segregation* is caused by the propagation of the species by means of seeds or germs any one of which, when developed, forms a community so related that the members breed with each other more frequently than with the members of other communities. If the constitution of any species is such that the ovules produced from one seed are more likely to be reached and fertilized by pollen produced from the same seed than by pollen produced from any other one seed, then Germinal Segregation is the result.

In order to secure this kind of Segregation it is not necessary that the flowers fertilized by pollen from the same plant should be more fertile, or the seeds capable of producing more vigorous plants than the flowers fertilized by pollen from another plant. All that is required is that of the seeds produced a larger number shall be fertilized by the pollen of the same plant than by the pollen of any other one plant.

This form of Segregation is closely related to Local Segregation on one side, and to Social Segregation on the other. It, however, differs from the former in that it does not depend on Migration or Transportation, and from the latter in that it does not depend on social instincts.

13. *Floral Segregation* is Segregation arising from the closest form of self-fertilization, namely the fertilization of the ovules of a flower by pollen from the same flower.

Many plants that in their native haunts are frequently crossed by the visits of insects depend entirely on self-fertilization when transported to other countries where no insect is found to perform the same service for them. The common pea (*Pisum sativum*) is an example of a species that habitually fertilizes itself in England, though Darwin found that it was very rarely visited by insects that were capable of carrying the pollen.* Darwin also mentions *Ophrys apifera* as an orchid which "has

* See 'Cross- and Self-Fertilization in the Vegetable Kingdom,' p. 161.

almost certainly been propagated in a state of nature for thousands of generations without having been once intercrossed." *

General Observations on Germinal and Floral Segregation.

A fact of great importance in its bearing on the origin of varieties should be here noted. Any variation, arising as a so-called sport, in any group of plants where either of these principles is acting strongly will be restrained from crossing, and will be preserved except in so far as reversion takes place. Now there is always a possibility that some of the segregating branches of descent will not revert, and that, through the special character which they possess in common, they will some time secure the services of some insect that will give them the benefit of cross-fertilization with each other without crossing with other varieties. The power of attaining new adaptations may be favoured by self-fertilization occasionally interrupted by interbreeding with individuals of another stock; for the latter is favourable as introducing vigour and variation, and the former as giving opportunity for the accumulation of variations.

(*b*) Impregnational Segregation.

Impregnational Segregation is due to the different relations in which the members of a species stand to each other in regard to the possibility of their producing fertile offspring when they consort together.

In order that Impregnational Segregation should be established and perpetuated it is necessary, 1st, that variation should arise from which it results that those of one kind are capable of producing vigorous and fertile offspring in greater numbers when breeding with each other than when breeding with other kinds; 2nd, that mutually compatible forms should be so brought together as to ensure propagation through a series of generations. In order to secure this second condition, it is necessary that, in the case of plants, there should be some degree of Local, Germinal, or Floral Segregation, and, in the case of animals that pair, either pronounced Local Segregation, or partial Local Segregation supplemented by Social or Sexual Segregation. The first of these factors I call Negative Segregation, as contrasted with all

* See 'Cross- and Self-Fertilization in the Vegetable Kingdom,' p. 439.

other forms of Segregation, which I group together as Positive Segregation.

Of each form of Segregation which we have up to this point considered, the segregating cause has been one that distributes individuals of the same species in groups between which free intergeneration is checked; while the propagation of the different groups depends simply on the original capacity for intergenerating common to all the members of the species. The intercrossing has been limited not by the capacity, but by the opportunity and inclination of the members. Coming now to cases in which the lack of capacity is the cause that checks the production of mongrels, we find a dependence of a very different kind; for to ensure the propagation of the different groups it is not enough that the general opportunity for the members to meet and consort remains unimpaired. There must be some additional segregating influence bringing the members together in groups corresponding to their segregate capacity, or they will fail of being propagated.

A partial exception must be made in the case of Potential and Prepotential Segregation, the latter being due to the prepotency of the pollen of a species or variety on the stigma of the same species or variety, and the former to the complete impotence of the foreign pollen. When allied species of plants are promiscuously distributed over the same districts, and flowering at the same time, prepotency of this kind is one of the most direct and efficient causes of Segregate Breeding. The same must be true of varieties similarly distributed whenever this character begins to affect them. In the case, however, of dicœcious plants and of plants whose ovules are incapable of being impregnated by pollen from the same plant, no single plant can propagate the species. If, therefore, the individuals so varying as to be prepotent with each other are very few and are evenly distributed amongst a vast number of the original form, they will fail of being segregated through failing to receive any of the prepotent pollen. It is thus apparent that when the mutually prepotent form is represented by comparatively few individuals, their propagation without crossing will depend on their being self-fertile and subject to Germinal or Floral Segregation, or on their being brought together by some other form of Positive Segregation.

When a considerable number of species of plants are commingled

and are flowering at the same time, their separate propagation is preserved, in no small degree, by the Prepotential Segregation of those that are most nearly allied, and by the complete Potential Segregation of those that belong to different families, orders, and classes. The same principle must come in to prevent the crossing of different species, genera, families, and orders of animals whose fertilizing elements are distributed in the water. We must, therefore, consider it a form of Positive as well as Negative Segregation; for the free distribution of the fertilizing element, with the superior affinity of the two sexual elements when produced by those that are mutually prepotential, secures the interbreeding of those that are mutually prepotential.

Impregnational Segregation generally exists between the different species of the same genus, almost always between species of different genera, and always between species of different families, orders, classes, and all groups of higher grade. And in all these cases it is associated with other forms of segregation, and whenever it has once become complete, it has never been known to give way. Though complete mutual sterility never gives place to complete mutual fertility, in every case where the descendants of the same stock have developed into different classes or orders, and in most cases where they have developed into different families or genera, the reverse process has taken place, and complete mutual fertility has given place to complete mutual sterility.

Under Impregnational Segregation I distinguish five principles: namely, Segregate Size, Segregate Structure, Potential and Prepotential Segregation, Segregate Fecundity, and Segregate Vigour.

14. *Segregate Size* is caused by incompatibility in size or dimensions.

As familiar illustrations of this form of Segregation, I may mention the following:—The largest and smallest varieties of the ass may run in the same pasture without any chance of crossing. I have also kept Japanese bantam fowls in the same yard with other breeds without any crossing. In many other species individuals of extreme divergence in size are incapable of interbreeding.

15. *Segregate Structure* is caused by the lack of correlation in the proportionate size of different organs and by other incompatibilities of structure.

Darwin suggests that the impossibility of a cross between

certain species may be due to a lack of correspondence in length of the pollen-tubes and pistils. Such a lack of harmony would perhaps account for difference of fertility in reciprocal crosses.

Segregate Structure does not usually arise till other forms of Segregation have become so well established that difference of structure does not make any essential difference in the amount of intergeneration. It is not, however, impossible that species that would otherwise be fertile *inter se* are thus held apart. In Broca's work on 'Human Hybridity' * there is a passage quoted from Prof. Serres, showing that it is very possible that this form of incompatibility may exist between certain races of man.

16. *Potential Segregation and Prepotential Segregation.*—These are caused by more or less free distribution of the fertilizing element together with the greater rapidity and power with which the sexual elements of the same species, race, or individual combine, as contrasted with the rapidity and power with which the elements of different species, races, or individuals combine. Potential Segregation is caused by the mutual impotence of the contrasted forms, as is always the case between different orders and classes; and Prepotential Segregation is caused by the superior influence of the fertilizing element from the same species, race, or individual, as contrasted with that from any other species, race, or individual, when both are applied to the same female at the same time, or sometimes when the prepotent element is applied many hours after the other.

For the operation of this principle the fertilizing element from different males must be brought to the same female.

When pollen from a contrasted genus, order, or class has no more effect than inorganic dust, it seems appropriate that we should call the result Potential Segregation rather than Prepotential Segregation, which implies that the foreign as well as the home pollen is capable of producing impregnation. Prepotential Segregation may be considered the initial form of Potential Segregation, the former passing through innumerable grades of intensity into the latter. We may, therefore, consider the principles as fundamentally one, though it will be convenient to retain both names.

* English translation published by the Anthropological Society of London, p. 28.

The importance of this principle in producing and preserving the diversities of the vegetable kingdom can hardly be overstated. If pollen of every kind were equally potent on every stigma, what would the result be? What distinctions would remain? And if Potential Segregation is necessary for the preservation of distinctions, is it not equally necessary for their production? Amongst water-animals that do not pair, the same principle of Segregation is probably of equal importance. Concerning this form of Segregation many questions of great interest suggest themselves, answers to which are not found in any investigations with which I am acquainted. Some of these questions are as follows :—

(1) Are there many cases of Prepotential as well as of Potential Segregation between different forms of water-animals?

(2) Is Prepotential Segregation always accompanied by Segregate Fecundity and Segregate Vigour?

(3) If not always associated, which of the three principles first appears? And what are their relations to each other?

(4) When allied organisms are separated by complete Environal Segregation, are they less liable to be separated by these three principles?

Darwin has in several places referred to the influence of prepotency in pollen, and in two places I have found reference to the form of prepotency that produces segregation; but I find no intimation that he regarded this or any other form of segregation as a cause of divergent evolution, or as a necessary condition for the operation of causes producing divergent evolution. The effect of prepotency in pollen from another plant in preventing self-fertilization is considered in the tenth chapter of his work on 'Cross- and Self-Fertilization in the Vegetable Kingdom,' pp. 391–400. Some very remarkable observations concerning the prepotency of pollen from another variety from that in which the stigma grows are recorded in the same chapter; but no reference is there made to the effect that must be produced when the pollen of each variety is prepotent on the stigma of the same variety. In the sixteenth chapter of 'Variation under Domestication,' it is suggested that prepotency of this kind might be a cause of different varieties of double hollyhock reproducing themselves truly when growing in one bed; though there was another cause to which the freedom from crossing in this case had been attributed. Again, in chapter viii. of the

fifth edition * of 'The Origin of Species,' in the section on "The Origin and Causes of Sterility," Darwin, while maintaining that the mutual sterility of species is not due to Natural Selection, refers to prepotency of the kind we are now considering as a quality which, occurring in ever so slight a degree, would prevent deterioration of character, and which would therefore be an advantage to a species in the process of formation, and accordingly subject to accumulation through Natural Selection. In order to construct a possible theory for the introduction of sterility between allied species by means of Natural Selection, he finds it necessary simply to add the supposition that sterility is directly caused by this prepotency. He, however, for several reasons concludes that there is no such dependence of mutual sterility on the process of Natural Selection. Concerning the prepotency he makes no reservation, and I accordingly judge that he continued to regard it as strengthened and developed through the action of Natural Selection.

It is concerning this last point that I wish to give reasons for a different opinion. I believe that qualities simply producing Segregation can never be accumulated by Natural Selection; for:—

(1) When separate generation comes in between two sections of a species they cease to be one aggregate, subject to modification through the elimination of certain parts. Both will be subject to similar forms of natural selection only so long as the circumstances of both and the variations of both are nearly the same, but they will no longer be the members of one body between which the selecting process is carried out. On the contrary, if they occupy the same district each group will stand in the relation of environment to the other, modifying it, and being modified by it, without mutually sharing in the same modification.

(2) Though one may exterminate the other, the change that comes to the successful group through the contest is not due to its superiority over the other, but to the superiority of some of its own members over others.

(3) When any Segregate form begins to arise we cannot attribute its success to the advantage of segeneration, for the inter-

* Since my comments on this passage were written, I have discovered that Darwin has omitted it from the sixth edition.

generating forms are at the same time equally successful; wherefore it is not the success, but the separateness of the success, that is due to the segeneration.

(4) The continuance of the descendants of a group in a special form will depend on its Segregation; but this is a very different thing from the special success of its descendants. The preservation of a *special kind* of adaptation is never due to natural selection, which is the superior success of the higher *degrees* of adaptation of every kind.

(5) The power of migration, or any other power directly related to the environment, may be accumulated by natural selection, and afterward lead to Segregation; but, according to my method of judging, the continuous advantage of Segregation over Integration can never be shown, for both are equally essential in the economy of nature; and though one process may at one time predominate over the other, the comparative advantage of Segregation, if there be such advantage, cannot be the cause of the preservation of forms endowed with segregative qualities, for they will certainly be preserved as long as they are able to win a bare existence, which is often a lower grade of success than the one from which they are passing.

(6) According to my view, instead of the accumulation of the Segregative prepotency depending on natural selection, the accumulation of divergent forms of natural selection depends on some form of Segregation.

But if the accumulation of Prepotential Segregation is not due to Natural Selection, how shall we explain it? It is, I think, due to the fact that those forms that have the most of this character are, through its action, caused to breed together. We have already seen, when considering Seasonal and Sexual Segregation, that, if Segregation is directly produced by the instincts or physiological constitution of the organism, there is a tendency toward an increasing manifestation of the character in successive generations. Those that have but a slight degree of Segregate prepotency eventually coalesce, forming one race, while those possessing the same character in a higher degree remain more distinct, and their descendants become still more segregate and still more permanently divergent. As long as the segregate forms are able to maintain vigour and secure fair sustentation, the process continues and the separation becomes more pronounced. Of this form of the Law of Cumulative Segregation

we may say that, as the descendants of the best fitted necessarily generate with each other and produce those still better fitted, so the descendants of those possessing the most segregative endowments necessarily generate with each other and produce those that are still more segregate.

It may at first appear that a slight degree of prepotence will prevent crossing as effectually as a higher degree; but further reflection will show that the efficiency of the prevention will vary in direct proportion with the length of time over which the prepotent pollen is able to show its prepotence, and this will allow of innumerable grades. If, in the case of certain individuals, the prepotency is measured by about twenty minutes, while with other individuals it enables the pollen of the same variety to prevail, though reaching the stigma an hour after the pollen of another variety has been applied, the difference in the degree of Segregation will be sufficient to make the persistence of the latter much more probable than that of the former. This form of Segregation is evidently one of the important causes preventing the free crossing of different species of plants. It probably has but little influence on terrestrial animals; but how far it is the cause of Segregation among aquatic animals is a question of no small interest, concerning which I have but small means for judging. I have, however, no hesitation in predicting that, unless we make the presence of this Segregative quality the occasion for insisting that the forms so affected belong to different species, we shall find that amongst plants the varieties of the same species are often more or less separated from each other in this way. I do not know of any experiments that have been directed toward the determining of this point; but on the general principle that physiological evolution is not usually abrupt, and that race distinctions are the initial forms under which specific differences present themselves, I can have no doubt that feeble prepotence precedes that which is more pronounced, and that part of this divergence in many cases takes place, while the divergent branches may be properly classed as varieties. Another reason for believing that Prepotential Segregation will be found on further investigation to exist in some cases between varieties, is the constancy with which, in the case of species, this character is associated with Segregate Fecundity and Segregate Vigour, which we know are sometimes characteristics of varieties in their relation to each other. The importance of these latter principles when occurring

in connection with different forms of partial Segregation will now be considered.

17, 18. *Segregate Fecundity and Segregate Vigour.*—By Segregate Fecundity I mean neither Segregation produced by Fecundity nor Fecundity produced by Segregation, but the relation in which species or varieties stand to each other when the intergeneration of members of the same species or variety results in higher fertility than the crossing of different species or varieties. In like manner Segregate Vigour is the relation in which species or varieties stand to each other when the intergeneration of members of the same species or variety produces offspring more vigorous than those produced by crossing with other species or varieties. Integrate Fecundity and Integrate Vigour are the terms by which I indicate the relation to each other of forms in which the highest fertility and vigour are produced by crossing, and not by independent generation.

Before discussing these principles through which the influence of Segregation is greatly increased, it will be an advantage if we can gain some idea of the nature of Cumulative Fertility in its relations to a law of still wider import. I refer to the fourfold law of antagonistic increase and mutual limitation between (1) Integration, (2) Segregation, (3) Adaptation, (4) Multiplication—in other words between (1) General invigoration and power of variation through crossing, (2) The opening of new opportunities and independent possibilities, (3) Special adaptation to present circumstances, (4) Powers of multiplied individualization. Darwin has considered at length the 1st and the 3rd, though I do not remember that he has anywhere pointed out that their development is due to a kind of self-augmentation. I believe this is so emphatically the case that the former might well be called the law of Self-Cumulative Vigour, and the latter the law of Self-Cumulative Adaptation. Corresponding to these two laws, I find the additional laws of Self-Cumulative Segregation and Self-Cumulative Fertility. Darwin's theory, that Diversity of Natural Selection is directly and necessarily dependent on exposure to different external conditions, tends to obscure, though not to deny, the fact that the breeding together of the better adapted, which causes the increase of adaptation, is due to the different degrees of endowment in the organism, rather than to diversity in the environment. It is also true of segregative endowment and of fertility that they are necessarily cumulative whenever

they belong in different degrees to members of the same Intergenerant that are equally fitted. The cumulation of vigour, as that of adaptation, is, I think, rightly classed as a form of Selection; for in both cases it depends on the power of the more highly endowed to supplant the less endowed without allowing them full opportunity to propagate; but the increase of segregative endowments and of fertility is due to principles quite different from this, and differing from each other. The segregative endowments augment through the inherent tendency of the more highly endowed to breed more exclusively with those of the same form, and therefore in the long run to breed more exclusively with each other; while the fertility of the more fertile neither drives out the less fertile nor holds the two classes apart, but simply multiplies the offspring of the more fertile, making it sure that in each generation they will predominate.

But all these forms of augmentation correspond in that they secure the breeding together of those possessing higher degrees of the special endowment, and so increase the average endowment, either of the whole number of the offspring, or of the segregated portion. Vigour increases through the breeding together of the more vigorous, resulting from their overcoming and crowding out the less vigorous without allowing them full opportunity to propagate. Adaptation increases through the breeding together of the better adapted, resulting from their supplanting their rivals without allowing them full opportunity to propagate. Segregative endowments increase through the breeding together of the more highly endowed, resulting from the fact that as long as Segregation is incomplete more than half of each generation of pure descent are necessarily the offspring of parents whose segregative endowments were above the average. Fertility increases through the breeding together of the more fertile, resulting from the fact that more than half of each generation are the offspring of parents of more than average fertility. As the breeding together of the more vigorous and the better adapted, caused by their superior success, tends to increase and intensify the vigour and adaptation of successive generations, so the breeding together of those more highly endowed with Segregative powers, caused by the Segregation, tends to strengthen and intensify the Segregative powers in successive generations; and so the breeding together of the more fertile, caused by the larger proportion of offspring produced by the more fertile, tends to increase the fertility of

successive generations. Among those that would be equally productive if equally nourished, the ratio of propagation varies directly as the degree of sustentation above a certain minimum (and perhaps below a certain maximum), and therefore directly as the degree of adaptation that secures this sustentation. This *propagation according to degrees of adaptation to the environment is what I understand by natural selection.* But among those that are equally adapted to the environment the ratio of propagation varies directly as the ratio of fertility. This *propagation according to degrees of fertility is what I call the Law of Cumulative Fertility.* It is not due to different degrees of success, or to any advantage which the individuals of one form have over those of other forms; but simply to the higher ratio of multiplication in the more fertile forms securing the intergeneration of the more fertile. *In connection with natural selection it ensures, in the descendants, the predominance of the better adapted of the more fertile, and the more fertile of the better adapted.*

At the close of the previous chapter I called attention to the fact that innumerable Local Segregations and other imperfect forms of Segeneration are being constantly broken down, partly by the increase of numbers and partly by the superior fertility and vigour of offspring produced by crossing. It seems to be a fundamental law that vigour and variation in the offspring depend on some degree of diversity of constitution in the parents, and diversity of constitution that is not entirely fluctuating depends on some degree of Positive Segregation; therefore vigour and variation depend on the breaking-down of incipient Segregations, and on the interfusion of the slightly divergent forms that had been partially segregated. But in the history of every race that is winning success by its vigour and variation there is liable to come a time when some variety, inheriting sufficient vigour to sustain itself, even if limited to the benefits of crossing with the individuals of the same variety, becomes partially Segregated. As we have already seen, Segregation, in so far as it depends on the qualities of the organism, tends ever to become more and more intense; but, in the very nature of things, not only will the Segregation be for many generations only partial, but partial Segregation, though it may greatly delay the submerging of different groups in one common group, will never prevent that result being finally reached. Though the siphon that connects two tanks of water be ever so

small, the water will in time find a common level in both tanks, unless there are additions or subtractions of water that prevent such a result. So, in the case under consideration, final fusion will take place, unless differentiation progresses more rapidly than the fusion, or some other influence comes in to counteract the levelling influence of occasional crosses. If, under such conditions, some branch of the partially Segregated variety becomes more fertile when generating with members of the same variety, and less fertile when generating with other varieties, a principle will be introduced tending to strengthen any form of partial Segregation that already exists between the varieties. This principle when co-operating with partial Segregation will produce pure masses of each variety, when, without the action of this principle, all distinctions would be absorbed by the crossing. We know that a transition from Integrate Fecundity to Segregate Fecundity usually takes place at a point in the history of evolution intermediate between the formation of an incipient variety and a strongly-marked species; and though the causes that produce this transition may be very difficult to trace, I believe the results that must follow can be pointed out with considerable clearness and certainty.

Darwin's investigations have shown that in many cases, if not in the majority, the relation of varieties to each other is that which I have called Integrate Fecundity and Integrate Vigour; that is, the highest fertility is attained when varieties are crossed, and the vigour of offspring thus produced is greater than when the intergeneration is within the limits of one variety. He, however, gives in 'Variation under Domestication,' chapter xvi., some special cases, in which "varieties of the same species behave, when crossed, like closely allied but distinct species"; and remarks that similar cases "may not be of very rare occurrence; for the subject has not been attended to." The same cases are also mentioned in all the editions of the 'Origin of Species.' *

The problems that arise in considering the different results produced by different degrees of Positive Segregation and Segregate Fecundity are of a nature suitable for mathematical treatment. Before, however, computing the effects of Segregate Fecundity when co-operating with Positive Segregation, it will be in place to show that it is of itself only a negative form of

* See 1st edition, p. 238; 5th edition, p. 259; 6th edition, p. 258.

Segregation, having no power to ensure the propagation of the varieties thus characterized, though they are fully adapted to the environment. This is most easily brought to light by considering the effect of a high degree of this quality when Positive Segregation is entirely wanting, or when it is sufficient to give simply a chance of Segregate Breeding by bringing each individual near to its natural mate. For example, let us suppose, 1st, that a male and a female each of several allied but mutually sterile species are brought together on one small island, all other tendences to Positive Segregation being removed, while mutual sterility still remains; 2nd, that a male and female when once mated remain together for the breeding-season; and 3rd, that all find mates. Now, if we have 7 species, each represented by one individual of each sex, what is the probability that all the species will be propagated? And what the probability for the propagation of none, or of but one, or of but two, or of but three of the species? The answers, as I have computed them, are as follows:—The probability that none will be propagated is $\frac{1854}{5040}$; that 1 species will be is $\frac{1855}{5040}$; that 2 species $\frac{924}{5040}$; that 3 species $\frac{315}{5040}$; that 4 species $\frac{70}{5040}$; that 5 species $\frac{21}{5040}$; that 7 species $\frac{1}{5040}$. These numerators are found in the 7th line of a table of figures which I call the Permutational Triangle. If we have 10 species, the probability that in any one trial no species will match truly and be propagated is $\frac{1334961}{3628800}$; that 1 species will match truly and propagate is $\frac{1334960}{3628800}$; that 10 will is $\frac{1}{3628800}$. This means that if 3,628,800 trials are made, one of them will probably be a case in which each male pairs with the female of the same species, while 1,334,961 will be cases in which none are so matched, and 1,334,960 will be cases in which one pair is so matched. It therefore appears that more than $\frac{8}{11}$ of the probabilities are against the continuance of more than one of the ten species.

There will perhaps be some hesitation in receiving these figures before I have given the method by which the results have been reached; but the necessary length of this paper, even when restricted to the briefest discussion of general principles, induces me to reserve my computations for another occasion. It is not, however, necessary to have a complete solution of this problem, in order to reach the conclusion that the origin of separate races and species depends not only upon their adaptation to the environment and their mutual sterility when

crossing with each other, but also upon their Positive Segregation. We can further see (when considering an extreme case, like either of the above-supposed cases) that Segregate Fecundity, without the aid of Positive Segregation, must lead to extinction. We have already seen that partial Segregation cannot by itself prevent the fusion of species. It therefore follows that in order to account for the continuance of divergent races we must suppose either that the Segregation is complete, or that the divergent evolution is strong enough to more than counterbalance the influence of the occasional crossing, or that the partial Segregation is aided by Segregate Fecundity or Segregate Vigour.

Between the members of species belonging to different orders we find not only complete Segregation, but complete sterility when attempts at crossing are made; but hope of gaining an explanation of how these characteristics have arisen is found, not in the study of those cases in which the process has been completed, but in the study of the relations to each other of species and varieties that are characterized by partial Segregation and mutual sterility, that is not complete. Here, again, mathematical analysis will help us in understanding the subject. Though I have not succeeded in constructing a complete mathematical representation of all the grades of intermingling that will take place, I have found a general formula that gives a close approximation to the proportion in which two species will breed pure as contrasted with the proportion of first crosses and their descendants that will be produced, in any case in which the degree of Segregation and the ratios of fertility for the pure and crossed breeds are known. As my object is simply to show under what conditions the pure races will continue without being swamped by crossing, it is not necessary that I should follow the action and reaction between the three-quarter-breeds. I wish, however, to call attention to the fact that when the number of the pure forms and of the half-breeds is constantly decreasing, without a general decrease in the sum of the descendants, it is evident that the three-quarter-breeds and their descendants are increasing; and when a three-quarter-breed on one side crosses with a three-quarter-breed on the other side, the offspring will usually be about intermediate between the two species; therefore, where the two species are equally numerous, if we find that the pure forms will disappear through fusion, we

may expect that the three-quarter-breeds will also disappear through fusion.

In constructing my formula, it was found necessary to commence by placing in the 1st generation of the half-breeds a more or less arbitrary symbol; for the true symbol in each case is the final one reached in the nth generation when n is a very high number. The chief interest therefore centres in what can be accomplished through the use of this formula for the nth generation. It seems to me to furnish a method of reaching the final proportion of pure breeding that will be produced by any form of combination between Positive Segregation and Segregate Fecundity, and to give results that would require thousands of years of continuous experimenting to reach in any other way.

Method of using Table III. (see p. 255).

By supposing n to be an indefinitely high number, and by giving different values to M, m, and c, we shall have the the means of contrasting the number of the pure-breeds with that of the half-breeds, when the process has been long continued under different degrees of Positive Segregation and Segregate Fecundity.

In the first place let us take a case in which there is no Segregate Fecundity, that is $M=m$; and for convenience in computation let us make $M=1$, $m=1$. In every case where m is not larger than M the fraction $\frac{(1-2c)m}{M-Mc}$ is less than unity, and the sum of the geometrical progression of our formula will fall within the limits of a number that can be easily computed by the well-known formula $S=\frac{a}{1-q}$, in which a is the first number of the progression, which in this case is 1, and q is the fraction we are now considering. Supposing $c=\frac{1}{10}$, the fraction will be $\frac{(1-\frac{2}{10})1}{1-\frac{1}{10}}=\frac{8}{9}=q, \therefore S=\frac{a}{1-q}$ becomes $S=\frac{1}{1-\frac{8}{9}}=\frac{9}{9-8}=9$. This number 9 is therefore equal to the sum of this progression and can therefore be used as the value of the infinite progression in the formula for the nth generation when n is a very high number. Substituting these values we find that the nth generation of the half-breeds equals the nth generation of the pure forms, each being equal to $\frac{9}{10}$ of A $(M-Mc)^{n-1}$. $A(M-Mc)^{n-1}$ is a vanishing quantity, for $M-Mc$ is less than 1. Every form is therefore in time fused with other forms. But let us try higher

Table I.

Arithmetical Computation, showing the number of Half-breeds as contrasted with the Pure-breeds, when $\frac{9}{10}$ of each variety form unions among themselves and double with each generation, while the offspring of the $\frac{1}{10}$ that form mixed unions simply equal the number of the parents by which they are produced: in other words when $c=\frac{1}{10}$, M=2, m=1 (see Table II.).

Variety No. 1, Pure-breeds.				*Of what generation.*	*Half of the Half-breeds.*	*Three-quarter breeds on one side.*	*Variety No. 2, Pure-breeds.*
1,000	=	A	=	Initial number			1,000
1·8							
1,800	=	A(1·8)	=	1st generation.	100		1,800
1·8							
3,240	=	$A(1·8)^2$	=	2nd „	260	20	3,240
1·8							
5,832	=	$A(1·8)^3$	=	3rd „	532	72	5,832
$357·05=(1·8)^{10}$ computed by log.							
∴ 357,050	=	$A(1·8)^{10}$	=	10th „	35,688		357,050
$39,347·272=(1·8)^{18}$							
∴ 39,347,272	=	$A(1·8)^{18}$	=	18th „	3,934,725		39,347,272

Explanation of Table I.

The 2nd generation of the half-breeds is found by taking $\frac{9}{10}$ of the previous half-breeds, *i. e.* $100\times\frac{9}{10}=90$, and $\frac{1}{10}$ of the previous pure-breeds (the $\frac{1}{10}$ that form mixed unions), minus $\frac{1}{10}$ of the previous half-breeds (because $\frac{1}{10}$ of the half-breeds consort with an equal number of pure-breeds, and so produce not half-breeds but three-quarter-breeds), *i. e.* 180−10=170. Adding these two sums together we have 90+170=260=The 2nd generation of half-breeds.

As in this Table the computation commences without any half-breeds, the following generations of half-breeds are all a little less than $\frac{1}{10}$ as large as the corresponding generations of pure breeds. When, however, we come to the 18th generation the difference is less than one in a million, and we may consider the result as practically corresponding with the formula for the *n*th generation, given in Table III.

The Three-quarter-breeds are obtained by multiplying $\frac{1}{10}$ of the previous generation of half-breeds by 2, and adding to the result the sum of the previous generations of three-quarter-breeds. This of course gives a number too large; for some of the three-quarter-breeds will fail to breed with three-quarter-breeds. A closer expression of the proportion between pure-breeds and three-quarter-breeds is given in Tables VII. and VIII.

TABLE II.

Preliminary Formula for showing the Proportion of Half-breeds to Pure-breeds.

Let R= the ratio of pure breeding, *i. e.* the Segregation.
Let c= the ratio of cross-breeding.
Ex. When $_{1}^{9}{}_{0}$ of the unions are within the limits of the species and $_{1}^{1}{}_{0}$ of the unions are with an allied species R=$_{1}^{9}{}_{0}$, c=$_{1}^{1}{}_{0}$. R will always equal $1-c$.
Let M=the ratio of fertility in each generation for those that breed with their own kind.
Let m=the ratio of fertility in each generation for the cross-unions and for the hybrids when breeding together.
Let A=the initial number of individuals representing the pure species when the computation commences.

Number of individuals representing the Pure form.			*Number of individuals representing the Half-breeds.*
A	=	Initial number.	
A(RM)	=	1st generation.	1st generation=Acm.
A(RM)^2	=	2nd ,,	2nd ,, =(AcmR+A(RM)c−Acmc)×m.*
A(RM)^3	=	3rd ,,	2nd ,, =(AcmR−Acmc)m+Acm(RM).
A(RM)^4	=	4th ,,	2nd ,, =Acm(R−c)m+Acm(RM).

Substituting $(1-c)$ for R in the 2nd gen., we have
A(M−Mc)^2=2nd generation.

Substituting in this $(1-c)$ for R, we have
2nd generation=Acm(1−2c)m+Acm(M−Mc).

* The term AcmR represents the number of half-breeds that form unions among themselves, the offspring being half-breeds; A(RM)c represents the total number of pure-breeds of the 1st generation that form mixed unions; of these Acmc form unions with an equal number of half-breeds, and their offspring being three-quarter-breeds must be rejected; the remainder, namely A(RM)c−Acmc, form unions with the other race, and their offspring are half-breeds of the 2nd generation.

TABLE III.

Developed Formula for Segregation and Segregate Fecundity, giving the proportion of Half-breeds to Pure-breeds.

Pure-breeds.		*Half-breeds.*
A = Initial number.		
$A(M-Mc)$ = 1st generation.	1st generation	$=Amc$.
$A(M-Mc)^2$ = 2nd „	2nd „	$=Amc(1-2c)m+Acm(M-Mc)$.
$A(M-Mc)^3$ = 3rd „	3rd „	$=Amc((1-2c)m)^2+Acm(M-Mc)(1-2c)m+Acm(M-Mc)^2$.
$A(M-Mc)^4$ = 4th „	4th „	$=Amc((1-2c)m)^3+Acm(M-Mc)((1-2c)m)^2+Acm(M-Mc)^2(1-2c)m+Acm(M-Mc)^3$.
	4th „	$=Amc(M-Mc)^3\left(\frac{((1-2c)m)^3}{(M-Mc)^3}+\frac{((1-2c)m)^2}{(M-Mc)^2}+\frac{(1-2c)m}{(M-Mc)}+\frac{(M-Mc)^3}{(M-Mc)^3}\right)$.
$A(M-Mc)^n$ = nth „	nth „	$=Amc(M-Mc)^{n-1}\times\left(\left(\quad\right)^{n-1}+\left(\quad\right)+\left(\quad\right)^3+\left(\quad\right)^2+\left(\frac{(1-2c)m}{M-Mc}\right)^1+1\right)$.

1*st Rule.*—The Pure-breeds of any generation are found by multiplying the previous generation of pure-breeds by $M-Mc$, and the half-breeds of any generation are found by multiplying the previous generation of half-breeds by $(1-2c)m$ and adding the previous generation of pure-breeds multiplied by cm.

2*nd Rule.*—The nth generation of pure-breeds $=A(M-Mc)^n=A(M-Mc)^{n-1}\times(M-Mc)$; and the nth generation of half-breeds $=Amc(M-Mc)^{n-1}$ multiplied by the sum Σ of the series $1+\frac{(1-2c)m}{M-Mc}+\ldots\ldots$, containing as many terms as that expressed by the number of the generation, *i. e.* containing n terms, of which the first is 1; $\therefore \frac{H}{P}=\frac{mc}{M-Mc}\Sigma\left(1+\frac{(1-2c)m}{M-Mc}+\ldots\ldots\right)$; H being the number of Half-breeds, and P being the number of Pure-breeds.

3*rd Rule.*—To correct this formula, so that it shall indicate the proportions that will result when the relative vigour of pure and cross breeds is considered, we must substitute MV for M, and mv for m; V being the proportion of each generation of pure-breeds that grow to maturity and propagate, and v being the proportion of half-breeds that do the same.

degrees of Segregation. If we make $c=\frac{1}{100}$ or $\frac{1}{1000}$, we still find that Half-breeds= Pure-breeds, while the latter are constantly decreasing, which shows that imperfect Positive Segregation, without the aid of some quality like Segregate Fecundity, cannot prevent a species being finally fused with other species, as long as the whole number of each successive generation does not increase.

Let us now consider cases in which the Segregation is incomplete but Segregate Fecundity comes in to modify the result. Let $M=2$, $m=1$, $c=\frac{1}{10}$. Substituting these values in our formula, we shall find that the sum of the infinite progression is $\frac{2}{5}=\frac{18}{10}$. And $M-Mc=\frac{18}{10}$, which makes the half-breeds = the pure forms $\times cm$; and $cm=\frac{1}{10}$. Let $M=2$, $m=1$, $c=\frac{1}{100}$; then Half-breeds=Pure forms $\times\frac{1}{100}$. Let $M=2$, $m=1$, $c=\frac{1}{2}$; then the infinite progression=1, $M-Mc=1$, and the pure forms in each generation will equal A, and the half-breeds $A\times\frac{1}{2}$. Therefore Half-breeds=Pure-breeds $\times\frac{1}{2}$.

Let $M=3$, $m=2$, $c=\frac{1}{2}$; then the sum of the infinite progression=1, and the Half-breeds $=\frac{1}{2}\times 2\times A(M-Mc)^{n-1}$, and the Pure-breeds $=1\frac{1}{2}\times A(M-Mc)^{n-1}$; therefore Half-breeds= Pure-breeds $\times\frac{2}{3}$.

Let $M=3$, $m=2$, $c=\frac{1}{3}$; then Half-breeds=Pure-breeds $\times\frac{2}{4}$.

Let $M=3$, $m=2$, $c=\frac{1}{4}$; then Half-breeds=Pure-breeds $\times\frac{2}{5}$.

Let $M=3$, $m=2$, $c=\frac{1}{5}$; then Half-breeds=Pure-breeds $\times\frac{2}{6}$.

Let $M=3$, $m=2$, $c=\frac{1}{10}$; then Half-breeds=Pure-breeds $\times\frac{2}{11}$.

Let $M=3$, $m=2$, $c=\frac{1}{100}$; then Half-breeds = Pure-breeds $\times\frac{2}{101}$.

TABLE IV.

Simplified Formulas for the Proportions in which Half-breeds and Three-quarter-breeds stand to Pure-breeds when all are equally vigorous.

From Table III. we learn that

$$\frac{H}{P}=\frac{mc}{M-Mc}\times\left(1+\frac{(1-2c)m}{M-Mc}+\ \ldots\ \right).$$

Whem $(1-2c)m$ is less than $M-Mc$, the series within the brackets is a decreasing geometrical progression, and we may obtain the value of the whole series by the formula $S=\frac{a}{1-q}$. Applying this formula we have

$$\frac{H}{P}=\frac{mc}{M-Mc}\times\frac{1}{1-\frac{(1-2c)m}{M-Mc}}$$

$$= \frac{mc}{M-Mc} \times \frac{M-Mc}{M-Mc-m+2mc}$$

$$= \frac{mc}{M-m+(2m-M)c}. \quad \ldots\ldots\ldots \text{(Formula 1)}$$

$$\therefore H = P \times \frac{mc}{M-m+(2m-M)c}. \quad \ldots\ldots\ldots (2)$$

If m' = the ratio of fertility for the Three-quarter-breeds, then according to the reasoning given in Tables VII. and VIII.,

$$\frac{T}{H} = \frac{2m'c}{M-m'+(2m'-M)c}; \quad \ldots\ldots\ldots (3)$$

and

$$\frac{T}{P} = \frac{H}{P} \times \frac{T}{H}. \quad \ldots\ldots\ldots (4)$$

The following solutions, as well as those given in Table V., are obtained by substituting values for M, m, and c in formula (2) :—

When M=4, m=3, then if

$c = \frac{1}{2}$, Half-breeds = Pure-breeds $\times \frac{3}{4}$,
$c = \frac{1}{3}$, ,, = ,, $\times \frac{3}{5}$,
$c = \frac{1}{4}$, ,, = ,, $\times \frac{3}{6}$,
$c = \frac{1}{5}$, ,, = ,, $\times \frac{3}{7}$,
$c = \frac{1}{6}$, ,, = ,, $\times \frac{3}{8}$,
$c = \frac{1}{7}$, ,, = ,, $\times \frac{3}{9}$,
$c = \frac{1}{8}$, ,, = ,, $\times \frac{3}{10}$,
$c = \frac{1}{9}$, ,, = ,, $\times \frac{3}{11}$,
$c = \frac{1}{10}$, ,, = ,, $\times \frac{3}{12}$,
$c = \frac{1}{100}$, ,, = ,, $\times \frac{3}{1002}$.

When M=5, m=4, then if

$c = \frac{1}{2}$, Half-breeds = Pure-breeds $\times \frac{4}{5}$,
$c = \frac{1}{3}$, ,, = ,, $\times \frac{4}{6}$,
$c = \frac{1}{4}$, ,, = ,, $\times \frac{4}{7}$,
$c = \frac{1}{5}$, ,, = ,, $\times \frac{4}{8}$,
$c = \frac{1}{6}$, ,, = ,, $\times \frac{4}{9}$,
$c = \frac{1}{7}$, ,, = ,, $\times \frac{4}{10}$,
$c = \frac{1}{8}$, ,, = ,, $\times \frac{4}{11}$,
$c = \frac{1}{9}$, ,, = ,, $\times \frac{4}{12}$,
$c = \frac{1}{10}$, ,, = ,, $\times \frac{4}{13}$,
$c = \frac{1}{100}$, ,, = ,, $\times \frac{4}{103}$,
$c = \frac{1}{1000}$, ,, = ,, $\times \frac{4}{1003}$.

TABLE V.

When $M=10$,

	and $m=9$;	$m=8$;	$m=7$;	$m=6$;	$m=5$;	$m=4$;	$m=3$;	$m=2$;	$m=1$.
If $c=\frac{1}{2}$, then Half-breeds = Pure-breeds ×	$\frac{9}{10}$	$\frac{8}{10}$	$\frac{7}{10}$	$\frac{6}{10}$	$\frac{5}{10}$	$\frac{4}{10}$	$\frac{3}{10}$	$\frac{2}{10}$	$\frac{1}{10}$
If $c=\frac{1}{3}$, H = P ×	$\frac{9}{11}$	$\frac{6}{12}$	$\frac{7}{13}$	$\frac{6}{14}$	$\frac{5}{15}$	$\frac{4}{16}$	$\frac{3}{17}$	$\frac{2}{18}$	$\frac{1}{19}$
If $c=\frac{1}{4}$, H = P ×	$\frac{9}{12}$	$\frac{8}{14}$	$\frac{7}{16}$	$\frac{6}{18}$	$\frac{5}{20}$	$\frac{4}{22}$	$\frac{3}{24}$	$\frac{2}{26}$	$\frac{1}{28}$
If $c=\frac{1}{5}$, H = P ×	$\frac{9}{13}$	$\frac{8}{16}$	$\frac{7}{19}$	$\frac{6}{22}$	$\frac{5}{25}$	$\frac{4}{28}$	$\frac{3}{31}$	$\frac{2}{34}$	$\frac{1}{37}$
If $c=\frac{1}{6}$, H = P ×	$\frac{9}{14}$	$\frac{8}{18}$	$\frac{7}{22}$	$\frac{6}{26}$	$\frac{5}{30}$	$\frac{4}{34}$	$\frac{3}{38}$	$\frac{2}{42}$	$\frac{1}{46}$
If $c=\frac{1}{7}$, H = P ×	$\frac{9}{15}$	$\frac{8}{20}$	$\frac{7}{25}$	$\frac{6}{30}$	$\frac{5}{35}$	$\frac{4}{40}$	$\frac{3}{45}$	$\frac{2}{50}$	$\frac{1}{55}$
If $c=\frac{1}{8}$, H = P ×	$\frac{9}{17}$	$\frac{8}{24}$	$\frac{7}{31}$	$\frac{6}{38}$	$\frac{5}{45}$	$\frac{4}{52}$	$\frac{3}{59}$	$\frac{2}{66}$	$\frac{1}{73}$
If $c=\frac{1}{10}$, H = P ×	$\frac{9}{18}$	$\frac{8}{26}$	$\frac{7}{34}$	$\frac{6}{42}$	$\frac{5}{50}$	$\frac{4}{58}$	$\frac{3}{66}$	$\frac{2}{74}$	$\frac{1}{82}$
If $c=\frac{1}{100}$, H = P ×	$\frac{9}{108}$	$\frac{8}{206}$	$\frac{7}{304}$	$\frac{6}{402}$	$\frac{5}{500}$	$\frac{4}{598}$	$\frac{3}{696}$	$\frac{2}{794}$	$\frac{1}{892}$
If $c=\frac{1}{1000}$, H = P ×	$\frac{9}{1008}$	$\frac{8}{2006}$	$\frac{7}{3004}$	$\frac{6}{4002}$	$\frac{5}{5000}$	$\frac{4}{5998}$	$\frac{3}{6996}$	$\frac{2}{7994}$	$\frac{1}{8992}$

Observations on Table V.

This mathematical analysis of the effects of Positive Segregation and Segregate Fecundity when co-operating brings distinctly into view several important relations.

1st. Incomplete forms of Segregation, that avail little or nothing in preventing a form from being absorbed in the course of time, become very efficient when strengthened by moderate degrees of mutual sterility. Take, for instance, the line of the table in which $c=\frac{1}{100}$. If 1 in every 100 unions is a cross with some other form, the form will in time be overwhelmed, unless other causes come in to counteract; but here we see that, if Segregate Fecundity occurs in the ratio of 10 to 9, the pure form becomes 12 times as numerous as the half-breeds; and if in the ratio of 10 to 5, it becomes 100 times as numerous.

2nd. Again, if we take the proportional differences between the different terms of the top line opposite $c=\frac{1}{2}$, we shall find them very unlike the differences that appear in the bottom line opposite $c=\frac{1}{1000}$. In the former the first term is 9 times as large as the last; while in the latter the first term is more than 80 times as large as the last. This shows that when Segregation is intense, differences in the degree of Segregate Fecundity produce greater contrasts than the same differences do when the Segregation is slight.

3rd. A similar distinction is found when we compare the right-hand column with the left-hand column. The smallest term in the former is to the largest term in the same column as 1 to 899, while in the left-hand column the greatest difference is as 1 to 100. This shows that when Segregate Fecundity is strongly developed, differences in the degrees of Segregation produce greater contrasts than the same differences produce when the Segregate Fecundity is but slightly developed.

4th. Once more let us consider the relations to each other of the four terms that stand in the upper left-hand corner of the table. Suppose that of some one variety of a plant species, characterized by Prepotential Segregation and Segregate Fecundity, we have occurring in equal numbers four variations whose relations to other varieties are indicated by the figures given in these four terms, while in their relations to each other they are completely fertile and not Segregated. Which variation will leave the greatest number of pure offspring, that is the greatest number

of offspring belonging to the one variety to which the four variations alike belong? Evidently the variation represented by the fraction $\frac{8}{12}$ will have the greatest influence on the following generation. But as the supposed conditions allow of exact computation, let us look at the problem a little closer. If each variation numbers say a thousand individuals, then the number of each that will breed true will be as follows:—Of the one represented by $\frac{9}{10}$, 526 will breed true and 474 will cross,

$\frac{9}{11}$, 550	„	450	„
$\frac{8}{10}$, 555·5	„	444·5	„
$\frac{8}{12}$, 600	„	400	„

And the next generation of each kind will be as follows: multiplying the pure parents by 10, and the hybrid parents by 8 or 9, according to the value of m, we have of those represented by

$\frac{9}{10}$,	pure offspring	5260,	hybrids	4266,
$\frac{9}{11}$,	„	5500,	„	4050,
$\frac{8}{10}$,	„	5555,	„	3556,
$\frac{8}{12}$,	„	6000,	„	3200.

There can, therefore, be no doubt that under such conditions the average Prepotential Segregation and Segregate Fecundity of the next generation will be considerably advanced, and so with each successive generation till the average of the Pure forms is represented by the fraction $\frac{8}{12}$, and is surrounded by a circle of variations, of which one will be represented by the fraction $\frac{7}{16}$. And from this new point continuous advance will be made toward ever higher and higher grades of Segregation and Segregate Fecundity; though of course the process will be subject to antagonisms and limitations arising from the principles of Self-accumulating Vigour and Self-accumulating Adaptation. Let it, however, be carefully noted that we have in this process the manifestation of a new principle, for it rests not only on Self-accumulating Positive Segregation but on Self-accumulating Segregate Fecundity.

TABLE VI.

Formula for Segregation, Segregate Fecundity, and Segregate Vigour, giving the Proportion of Half-breeds to Pure-breeds. (Constructed from Table III., according to rule 3.)

Pure-breeds.		*Half-breeds.*
A	Initial number.	
$A(MV-MVc)$.	1st generation.	$Amvc$.
$A(MV-MVc)^2$.	2nd generation.	$Amvc(1-2c)mv+Amvc(MV-MVc)$.
$A(MV-MVc)^3$.	3rd generation.	$Amvc((1-2c)mv)^2+Amvc(MV-MVc)(1-2c)mv+Amac(MV-MVc)^2$.
$A(MV-MVc)^4$.	4th generation.	$Amvc((1-2c)mv)^3+Amvc(MV-MVc)((1-2c)mv)^2+Amvc(MV-MVc)^2(1-2c)mv+Amvc(MV-MVc)^3$. $=Amvc(MV-MVc)^3\left(\frac{((1-2c)mv)^3}{(MV-MVc)^3}+\frac{((1-2c)mv)^2}{(MV-MVc)^2}+\frac{((1-2c)mv)}{(MV-MVc)}+\frac{(MV-MVc)^3}{(MV-MVc)^3}\right)$.
$A(MV-MVc)^{n-1}$	$n-1$th generation.	
$A(MV-MVc)^n$	nth generation.	$Amvc(MV-MVc)^{n-1}\left(\frac{(1-2c)mv}{MV-MVc}\right)^{n-1}+\ldots+\left(\quad\right)^3+\left(\frac{(1-2c)mv}{MV-MVc}\right)^2+\frac{(1-2c)mv}{MV-MVc}+1\Big)$.

nth generation of Pure-breeds $=A(MV-MVc)^{n-1}\times(MV-MVc)$; and therefore $\frac{\text{Half-breeds}}{\text{Pure-breeds}}=\frac{mvc}{MV-MVc}\left(1+\frac{(1-2c)mv}{MV-MVc}+\ldots\right)$.

In the above formula, V = Vigour of Pure-breeds expressed by a fraction that gives the proportion of each generation that grow to maturity and propagate, v = the vigour of the Half-breeds expressed in the same way.

TABLE VII.

Formula for Segregation, Segregate Fecundity, and Segregate Vigour, giving the Proportion of the Three-quarter-breeds to the Pure-breeds.

T=the number of Three-quarter-breeds; m'=Ratio of Fertility for the same; v', a fraction giving the proportion of the Three-quarter-breeds that come to maturity. H=the number of Half-breeds. P=the number of Pure-breeds.

Turning to Table I., we find that the Three-quarter-breeds of each generation are the offspring of $\frac{1}{10}$ (or c) of the previous generation of Half-breeds who consort with an equal number of Pure-breeds, plus the descendants of previous generations of Three-quarter-breeds in as far as they breed with each other. Commencing our computation with the nth generation we know from Table VI., that the previous generation of Pure-breeds $=A\,(MV-MVc)^{n-1}$, and the Half-breeds of the same generation $=A(MV-MVc)^{n-1}\times\frac{H}{P}$; $\frac{H}{P}$ being the Ratio in which Half-breeeds stand to Pure-breeds, which is obtained as shown in Tables IV., V., and VI.; and c of this number will consort with an equal number of Pure-breeds, making $A(MV-MVc)^{n-1}\times\frac{H}{P}\,2c$ parents in the $n-1$th generation, that will produce $m'v'$ times that number of Three-quarter-breed offspring of the nth generation that will grow to maturity, Starting with this number in the nth generation, and pursuing the same method as was used in constructing Table III., we obtain the following series:—

Three-quarter-breeds.

nth generation $=A(MV-MVc)^{n-1}\frac{H}{P}2cm'v'$.

$(n+1)$th generation $=A(MV-MVc)^{n-1}\frac{H}{P}2cm'v'\times(1-2c)m'v'+A(MV-MVc)^{n}\frac{H}{P}2cm'v'$.

$(n+2)$th generation $=A(MV-MVc)^{n-1}\frac{H}{P}2cm'v'\left((1-2c)m'v'\right)^2+A(MV-MVc)^{n}\frac{H}{P}2cm'v'\left((1-2c)m'v'\right)+A(MV-MVc)^{n+1}\frac{H}{P}2cm'v'$.

$(n+n)$th generation $=A(MV-MVc)^{n-1}\frac{H}{P}2cm'v'(MV-MVc)^{n}\left(\left(\frac{(1-2c)m'v'}{MV-MVc}\right)^n+\ldots+\left(\frac{(1-2c)m'v'}{MV-MVc}\right)^2+\left(\frac{(1-2c)m'v'}{MV-MVc}\right)^1+\left(\frac{MV-MVc}{MV-MVc}\right)^n\right)$.

In the $(n+n)$th generation, $P=A(MV-MVc)^{n+n}$; and therefore $\frac{T}{P}=\frac{\frac{H}{P}2cm'v'}{MV-MVc}\left(1+\left(\frac{(1-2c)m'v'}{MV-MVc}\right)^1+(\quad)^2+(\quad)+(\quad)^n\right)$.

TABLE VIII.

Simplified Formulas, giving the Proportions in which Half-breeds and Three-quarter-breeds stand to Pure-breeds when we have both Segregate Fecundity and Segregate Vigour.

From Table VI. we learn that

$$\frac{H}{P}=\frac{mvc}{MV-MVc}\times\left(1+\frac{(1-2c)mv}{MV-MVc}+\ \ldots\right).$$

When the numerator, $(1-2c)mv$, is less than the denominator, $MV-MVc$, the sum of the whole series within the brackets may be obtained in accordance with the formula $S=\frac{a}{1-q}$, in which S = the sum of the series, a = the first term, and q = the constant multiplier.

$$\therefore\ \frac{H}{P}=\frac{mvc}{MV-MVc}\times\frac{1}{1-\frac{(1-2c)mv}{MV-MVc}}$$

$$=\frac{mvc}{MV-MVc}\times\frac{MV-MVc}{MV-MVc-mv+2mvc}$$

$$=\frac{mvc}{MV-mv+(2mv-MV)c}. \qquad \text{(Formula 1)}$$

Applying the same method to the formula in Table VII., we find that

$$\frac{T}{P}=\frac{H}{P}\times 2\times\frac{m'v'c}{MV-m'v'+(2m'v'-MV)c}.$$

$$\therefore\ \frac{T}{P}=\frac{H}{P}\times\frac{2m'v'c}{MV-m'v'+(2m'v'-MV)c}; \qquad (2)$$

and

$$\frac{T}{H}=\frac{2m'v'c}{MV-m'v'+(2m'v'-MV)c}. \qquad (3)$$

If $M=10$, $m=5$, $m'=5$, $V=\frac{1}{3}$, $v=\frac{1}{10}$, $v'=\frac{1}{10}$, $c=\frac{1}{10}$,

then $\frac{H}{P}=\frac{\frac{5}{100}}{\frac{10}{9}-\frac{5}{10}+(\frac{10}{10}-\frac{10}{9})\frac{1}{10}}=\frac{\frac{5}{100}}{\frac{100}{900}-\frac{45}{90}-\frac{1}{90}}=\frac{\frac{5}{100}}{\frac{54}{90}}=\frac{45}{540}=\frac{9}{108}=\frac{1}{12}$;

and (as $m=m'$, and $v=v'$)

$$\frac{T}{H}=2\frac{H}{P}=2\frac{1}{12}=\frac{1}{6}\ ;\ \text{and}\ \frac{T}{P}=\frac{H}{P}\times\frac{T}{H}=\frac{1}{12}\times\frac{1}{6}=\frac{1}{72}.$$

If $M=10$, $m=10$, $m'=10$, $V=\frac{1}{3}$, $v=\frac{1}{90}$, $v'=\frac{1}{90}$, $c=\frac{1}{10}$,

then $\frac{H}{P}=\frac{\frac{1}{900}}{\frac{10}{9}-\frac{10}{90}+(\frac{20}{900}-\frac{10}{9})\frac{1}{10}}=\frac{\frac{1}{900}}{\frac{100}{900}-\frac{100}{900}+\frac{2}{900}-\frac{10}{900}}=\frac{1}{82}$;

and $\frac{T}{H}=\frac{2}{82}=\frac{1}{41}$; and $\frac{T}{P}=\frac{H}{P}\times\frac{T}{H}=\frac{1}{3362}$.

In this latter case, where the Vigour of Hybrids is $\frac{1}{10}$ that of Pure-breeds, while their Fecundity is equal to that of Pure-breeds, we find $\frac{H}{P}=\frac{1}{82}$, which is the same result as that given in the 8th line of the last column of Table V., where the Fecundity of cross unions and of Hybrids is $\frac{1}{10}$ that of Pure-breeds, while their Vigour is equal.

The Influence of Segregate Vigour.

I think we may say we have here come in sight of one form of the still wider fourfold law already mentioned; for on the same principle that Segregate Fecundity increases when once allied with partial Segregation in vigorous forms, Segregate Vigour must also tend to increase when brought into the same alliance; and I believe it will be found that there is a similar principle tending to the self-accumulation of Segregate Adaptation.

At the point where they both arise, that is during the period that immediately follows the act of impregnation, it is difficult to distinguish between the two principles, and the mortality of the hybrid embryo before birth, or before it leaves the egg, may be conveniently classed as Segregate Fecundity. *

Though the two principles are so closely related, it would be a great mistake not to distinguish them; for there is no close correspondence between the degrees in which the two qualities occur in the relations of individuals or varieties; and in some cases we find Segregate Fecundity associated with Integrate Vigour. The mule, though absolutely sterile, possesses vigour equal, if not superior, to that of either parent. In the record of experiments given by Darwin in 'Cross- and Self-Fertilization in the Vegetable Kingdom' mention is made of certain species in which self-fertilized flowers are more fertile than the cross-fertilized, while the plants produced from the crossed seed are the more vigorous; and of other species in which cross-fertilized flowers are by far the most productive, while the plants produced from the crossed seed are neither taller nor heavier than the self-fertilized.† In the same work the common pea (*Pisum sativum*), the common tobacco (*Nicotiana tabacum*), and *Canna Warscewiczi* are shown to be more vigorous when raised from self-fertilized seed than when raised from seed crossed with other individuals of the same strain; but in the case of the tobacco and the pea, great increase of vigour is produced by a cross with a slightly different variety while the fertility is increased but little if any.

But the most interesting of all his experiments as bearing on the subject of Segregate Vigour, is given in the history of "*The Descendants of the self-fertilized Plant, named* Hero, *which appeared in the Sixth Self-fertilized Generation of* Ipomœa purpurea.' "A cross between the children of *Hero* did not give to the

* See 'Origin of Species,' 6th edition, p. 249. † See pages 322–329.

grandchildren any advantage over the self-fertilized grandchildren raised from the self-fertilized children." "And, what is far more remarkable, the great-grandchildren, raised by crossing the grandchildren with a fresh stock, had no advantage over either the intercrossed or the self-fertilized great-grandchildren. It thus appears that *Hero* and its descendants differed in constitution in an extraordinary manner from ordinary plants of the same species." "If we look to the [ordinary] plants of the ninth generation in table x., we find that the intercrossed plants [of the same stock] were in height to the self-fertilized as 100 to 79, and in fertility as 100 to 26; whilst the Colchester-crossed plants [raised by crossing with a fresh stock] were in height to the intercrossed as 100 to 78, and in fertility as 100 to 51."* The Colchester-crossed plants were therefore in height to the self-fertilized as 1 to $\cdot 78 \times \cdot 79$, or as 1000 to 616, and in fertility as 1 to $\cdot 51 \times \cdot 26$, or as 1000 to 133; while the self-fertilized descendants of *Hero* when crossed with the same fresh stock not only had no advantage over those that had been continuously self-fertilized for nine generations, but, as the details of the experiment show, the advantage was on the side of the plants raised from the self-fertilized seed. The experiment was conducted under conditions decidedly unfavourable for the production of healthy plants; but, as it is usually found that the superiority of crosses between varieties is most clearly brought to light when the competitors are subjected to unfavourable circumstances, it seems to furnish even stronger evidence of Segregate Vigour being occasionally produced in the earliest stages of divergent evolution, than would have been furnished if the same degree of superiority in the self-fertilized plants had been obtained under a less severe test. As the case is of unusual interest, I give the details as recorded by Darwin:—

"Several flowers on the self-fertilized grandchildren of *Hero* in table xvi. were fertilized with pollen from the same flower; and the seedlings raised from them (great-grandchildren of *Hero*) formed the ninth self-fertilized generation. Several other flowers were crossed with pollen from another grandchild, so that they may be considered as the offspring of brothers and sisters, and the seedlings thus raised may be called the intercrossed great-grandchildren. And, lastly, other flowers were fertilized with pollen from a distinct stock, and the seedlings

* 'Cross- and Self-Fertilization,' pp. 47, 60, 61.

thus raised may be called the Colchester-crossed great-grandchildren. In my anxiety to see what the result would be, I unfortunately planted the three lots of seeds (after they had germinated on sand) in the hothouse in the middle of winter, and in consequence of this the seedlings (twenty in number of each kind) became very unhealthy, some growing only a few inches in height, and very few to their proper height. The result, therefore, cannot be fully trusted; and it would be useless to give the measurements in detail. In order to strike as fair an average as possible, I first excluded all the plants under 50 inches in height, thus rejecting all the most unhealthy plants. The six self-fertilized thus left were on an average 66·86 inches high, the eight intercrossed plants 63·2 high, and the seven Colchester-crossed 65·37 high; so that there was not much difference between the three sets, the self-fertilized plants having a slight advantage. Nor was there any great difference when only the plants under 36 inches in height were excluded. Nor, again, when all the plants, however much dwarfed and unhealthy, were included.

"In this latter case the Colchester-crossed gave the lowest average of all; and if these plants had been in any marked manner superior to the other two lots, as from my former experience I fully expected they would have been, I cannot but think that some vestige of such superiority would have been evident, notwithstanding the very unhealthy condition of most of the plants. No advantage, as far as we can judge, was derived from intercrossing two of the grandchildren of *Hero*, any more than when two of the children were crossed. It appears therefore that *Hero* and its descendants have varied from the common type, not only in acquiring great power of growth and increased fertility when subjected to self-fertilization, but in not profiting from a cross with a distinct stock; and this latter fact, if trustworthy, is a unique case, as far as I have observed in all my experiments." *

Let us now consider for a moment what must be the result when such a variation occurs in a wild species subject to the ordinary conditions of competition. In the first place, it would gradually prevail over other representatives of the same local stock, both by its more vigorous growth and by its greater

* 'Cross- and Self-Fertilization in the Vegetable Kingdom,' pp. 50, 61.

fertility, especially in the case of flowers that failed of securing a cross. And afterwards, when it came into competition with the equally adapted variety from which it was partially protected by Segregate Vigour, it would neither be driven out nor lose its separate existence in a commingled race. It will be observed that we have in such a case Local, Germinal, and Floral Segregation, each producing partial effects which are enhanced by the Segregate Vigour. In order to bring out the relation of these factors to each other, let us assume definite values for each. Let us suppose that $\frac{3}{10}$ of the flowers are self-fertilized, $\frac{3}{10}$ are fertilized with pollen from another flower of the same plant, $\frac{3}{10}$ are fertilized with pollen from other plants of the same new variety, and $\frac{1}{10}$ are fertilized with pollen from the older variety occupying contiguous areas. Therefore the sum of the segregating influences, which is called the "Ratio of pure breeding," and is represented by R in Table II., equals $\frac{9}{10}$; and the "Ratio of cross-breeding," represented by c in all the tables, equals $\frac{1}{10}$. Again, let us suppose that the fertility of the pure breeds is the same as that of the half-breeds, but that the superior vigour of the former is such that any one of the pure seeds has twice as good a chance of germinating, growing to maturity, and producing seed as any one of the crossed seeds. The general effect on the final result will in that case be the same as if the "Ratio of increase for the pure unions" (which I call M) equalled 10, while the "Ratio of increase for the cross unions" (which I call m) equalled 5. Turning now to Table V., we can easily find the ratio in which the number of pure-breeds will stand to the half-breeds, if the conditions continue long; for in the column in which m equals 5 and in the line marked $c=\frac{1}{10}$ we find $\frac{5}{50}$, which means that the half-breeds will equal the pure-breeds multiplied by $\frac{5}{50}$, or by $\frac{1}{10}$.

Segregate Vigour and Segregate Fecundity between Human Races.

My attention has recently been called to the following facts relating to the Japanese and Aino races, who have for many centuries met under circumstances favourable for interfusion without any apparent effect of this kind. I quote from 'Memoirs of the Literature College, Imperial University of Japan,' No. 1: "The Language, Mythology, and Geographical Nomenclature of Japan viewed in the Light of Aino Studies," by Basil Hall Chamberlain, p. 43:—

"With what logic, it may be urged, do you invite us to accept a great extension of the Aino race in early Japan, when it is a physiological fact, vouched for by so high an authority as Dr. Baelz, that there is little or no trace of Aino blood in the Japanese people? In reply to this some would perhaps quote such examples as New England, whence the Indians have vanished, leaving nought behind them but their place-names. In Japan, however, the circumstances are different from those of New England. There has undoubtedly been constant intermarriage between the conquerors and the native race upon the Aino border. We can infer this from history. Those who have travelled in Yezo know it by personal experience to-day. Nevertheless, these intermarriages may well consist with the absence of any trace of Aino blood in the population. As a matter of fact, the Northern Japanese, in whose veins there should be most Aino blood, are no whit hairier than their compatriots in Central and Southern Japan. Anyone may convince himself of this by looking at the coolies (almost all Nambu or Tsugaru men) working in the Hakodate streets during the summer months, when little clothing is worn. But the paradox is only on the surface. The fact is that the half-castes die out—a fate which seems, in many quarters of the world, to follow the miscegenation of races of widely divergent physique. That this is the true explanation of the phenomenon was suggested to the present writer's mind by a consideration of the general absence of children in the half-breed Aino families of his acquaintance. Thus, of four brothers in a certain village where he staid, three have died leaving widows without male children, and with only one or two little girls between the three. The fourth has children of both sexes; but they suffer from affections of the chest and from rheumatism. Mr. Batchelor, whose opportunities for observation have been unsually great, concurs in considering this explanation as sufficient as it is simple. There are scores of mixed marriages every year. There are numerous half-breeds born of these marriages. But the second generation is almost barren; and such children as are born—whether it be from two half-breed parents, or from one half-breed parent and a member of either pure race, are generally weakly. In the third or fourth generation the family dies out. It may be added that the half-breeds have a marked tendency to baldness, and that their bodies are much less hairy than those of the genuine

Ainos. This fact has doubtless helped to cause the divergence of opinion with regard to Aino hairiness. For the comparatively smooth half-breeds usually speak Aino, dress Aino-fashion, and are accounted to be Ainos, so that travellers are likely to be misled, unless constantly on their guard. There seem to be half-breeds in all the villages whither Japanese pedlars and fishermen have penetrated. There have therefore probably, at some time or other, been half-breeds in every portion of Japan where the two races have come in contact."

If these two races were equal in civilization and in natural adaptation to the environment, or if one race was specially adapted to mountain life and the other to life by the sea-shore, it seems probable that they might permanently occupy adjoining countries without losing any of their distinctive characteristics. Broca, after careful collation of all the information that could be gathered from the publications of travellers and historians, reaches the conclusion "that alliances between the Anglo-Saxon race and the Australians and Tasmanians are but little prolific; and that the mulattoes sprung from such intercourse are too rare to have enabled us to obtain exact particulars as to their viability and fecundity."* I have no means of knowing whether later investigations in Australia and other parts of the world have thrown fuller light on the mutual fertility or sterility of the more divergent human races, but I am inclined to think that the interest in the subject has declined since Darwin has shown that such data can never afford proof that the different races of man are not descended from common ancestry. There are, however, signs that a renewed interest in the subject is being awakened through the realization that it has a direct bearing on the theory of the origin of species.

Impregnational Segregation a Cause of Divergence in both its Earlier and Later Stages.

As we have already seen, the negative factors† Segregate Vigour and Segregate Fecundity would tend to produce extinction if not associated with positive forms of Segregation. But

* See 'Phenomena of Hybridity in the Genus *Homo*.' By Paul Broca. English translation, published for the Anthropological Society of London by Longman, Green, Longman, and Roberts (1864), pp. 45–60.

† For a definition of Negative Segregation see page 238 of this paper.

in the case of organisms whose fertilizing elements are distributed by wind and water, the qualities that produce these negative forms of Segregation are usually accompanied by those that produce Prepotential Segregation, which is in an important degree positive. But even Prepotential Segregation, when produced by mutual incompatibility between a few individuals and a numerous parent stock, depends for its continuance and development on Local, Germinal, or Floral Segregation, partially securing the intergeneration of the few that are mutually compatible. On the one hand, Impregnational Segregation depends on some degree of Local, Germinal, or Floral Segregation which is a constant feature in most species; but, on the other hand, not only do these initial forms of Positive Segregation fail of producing any permanent divergence till associated with Impregnational Segregation, but the more effective forms of Positive Segregation, such as Industrial, Chronal, Fertilizational, Sexual, and Social Segregation, often depend on Impregnational Segregation, inasmuch as the divergence of endowments which produces these depends on Impregnational Segregation. Moreover, in all such cases, increasing degrees of diversity in the forms of adaptation, and consequently of diversity in the forms of natural selection, must also depend upon these negative factors, which in their turn depend on the weak, initial forms of Positive Segregation.

Divergent evolution always depends on some degree of Positive Segregation, but not always on Negative Segregation. Under Positive Segregation of a rigorous form (as, for example, complete Geographical Segregation), considerable divergence may result without any sexual incompatibility. Darwin has shown, by careful experiments, that *Integrate* Vigour and Fecundity is the relation in which the varieties of one species usually stand to each other. This fact does not, however, prove that the more strongly divergent forms, called species, which are prevented from coalescing by Segregate Vigour and Fecundity, did not acquire some degree of this latter character before any permanent divergence of form was acquired. Their having acquired this segregating characteristic may be the very reason why their forms are now so decidedly different, for without it they would have been swallowed up by the incoming waves of intergeneration. Again, we must remember that forms only moderately divergent are habitually classed as different species if they are separated by Segregate Vigour and Fecundity (that is by some degree of

mutual sterility), unless observation shows that they are of common descent. These two considerations sufficiently explain why the varieties of one species are so seldom reported as mutually infertile. Notwithstanding this, the experiments of Gartner and of Darwin, already referred to at length, seem to show that Segregate Fecundity and Vigour may arise between varieties that spring from one stock. In view of these cases, we must believe that in the formation of some, if not many, species, the decisive event with which permanent divergence of allied forms commences is the intervention of Segregate Fecundity or Vigour between these forms. Positive Segregation, in the form of Local, Germinal, or Floral Segregation producing only transitory divergences, always exists between the portions of a species that has many members, but as it does not directly produce the Negative Segregation which is, in such cases, the necessary antecedent of permanent divergence, we cannot, in accordance with the usage of language, call it *the* cause of the permanent divergence. Moreover, though it may be in accordance with ordinary language to call the Negative Segregation, which is the immediate antecedent of the permanent divergence, the cause of the same, it will be more correct to call the coincidence of the Negative and Positive Segregations the cause, and still more accurate to say that the whole range of vital activities (when subjected to the limitations of any sexual incompatibility that corresponds in the groups it separates to some previous but ineffectual Local, Germinal, or Floral Segregation), will produce permanent divergence.

In many cases not only is the entrance of Impregnational Segregation the cause of the commencement of permanent divergence, but its continuance is the cause of the continuance of the divergence. The clearest illustration of this is found in the case of plants that are fertilized by pollen that is distributed by the wind. All the higher, as well as the lower, groups of such plants would rapidly coalesce if each grain of pollen was capable of producing fertilization, with equal certainty, promptness, and efficiency, on whatever stigma it might fall. We may also be sure that, with organisms that depend upon water for the distribution of their fertilizing elements, Impregnational Segregation is an essential factor in the development of higher as well as of lower taxonomic groups.

It is important to observe that, in the cases under consideration, *the inferior fertility or vigour resulting from the crossing* of

the incompatible forms is as truly a cause of divergence as *the inferior opportunity for crossing* which from the first existed between the members occupying different localities or between the flowers growing on different trees of the same species. The former has been called Negative, and the latter Positive, Segregation, not for the sake of distinguishing different grades of efficiency, but for the sake of indicating the different methods of operation in the two classes of Segregation.

(*c*) Institutional Segregation.

Institutional Segregation is the Reflexive form of Rational Segregation. It is produced by the rational purposes of man embodied in institutions that prevent free intergeneration between the different parts of the same race.

As the principal object of the present paper is to call attention to the causes of Segregation acting independently of effort and contrivance directed by man to that end, it will be sufficient to enumerate some of the more prominent forms under which Institutional Segregation presents itself, noting that some of these influences come in as supplemental to the laws of segregation already discussed, simply reinforcing by artificial barriers the segregations that have their original basis in nature. The chief forms that should be enumerated are National, Linguistic, Caste, Penal, Sanitary, and Educational Segregation; and if we had not already considered Industrial Segregation in the previous chapter, that might be added.

Concluding Remarks.

Besides Artificial and Institutional Segregation, which depend on the rational purpose of man, we have now considered numerous forms of Segregation, resting on no less than 18 groups of purely natural causes. Owing to the length of this paper I deem it wise to bring it to a close without discussing the laws that cooperate in intensifying the effects directly produced by the segregative causes already considered. As I have shown in Chapter II., Segregation is not simply the Independent Generation of the different sections of a species, but the Independent Generation of sections that differ; and though no one will believe that any two sections of a species are ever exactly equivalent, it is evident that the degrees of difference may be greater

or less, and that whatever causes a greater difference in two sections that are prevented from intergenerating will also be a cause of increased Segregation.

It has been observed that some of the causes enumerated in this and the previous chapter are primarily separative, and that no one of those that are primarily segregative is at any one time segregative in regard to many classes of characters. As several forms of Segregation may co-operate in securing a given division of a species, and one form is superimposed upon another, the aggregate effect must be incalculably great; but we easily perceive that it may be indefinitely enhanced by causes producing increased divergence in the segregated branches. The causes which produce monotypic evolution when associated with Intergeneration must be equally effective in producing polytypic evolution when associated with Segeneration, whether in its separative or segregative forms. But the discussion of Intensive Segregation must be reserved for another occasion.

Believing that the study of Cumulative Segregation in its relations to the other factors of evolution will throw light on the origin of species far beyond what I have been able to elicit, I trust the subject will secure the attention of those who enjoy better opportunities than I do for carrying forward such investigations.

26 Concession, Osaka, Japan,
May 12, 1887.

APPENDIX.

Classified Table of Forms of Segregation.

A.

Environal Segregation.
- (*a*) Industrial Segregation.
  - Sustentational.
  - Defensive.
  - Nidificational.
- (*b*) Chronal Segregation.
  - Cyclical.
  - Seasonal.

(*c*) Spatial Segregation.

Geographical. } { Migrational.
Local. } { Transportational.
{ Geological.

(*d*) Fertilizational Segregation.

(*e*) Artificial Segregation.

B.

Reflexive Segregation.

(*a*) Conjunctional Segregation.
- Social.
- Sexual.
- Germinal.
- Floral.

(*b*) Impregnational Segregation.
- Segregate Size.
- Segregate Structure.
- Prepotential Segregation.
- Segregate Fecundity.
- Segregate Vigour.

(*c*) Institutional Segregation.

C.

Intensive Segregation.

(*a*) Assimilational Intension.

(*b*) Stimulational Intension.

(*c*) Suetudinal Intension.

(*d*) Correlated Intension.

(*e*) Integrational Intension.

(*f*) Selectional Intension.

(*g*) Fecundal Intension.

(*h*) Eliminational Intension.