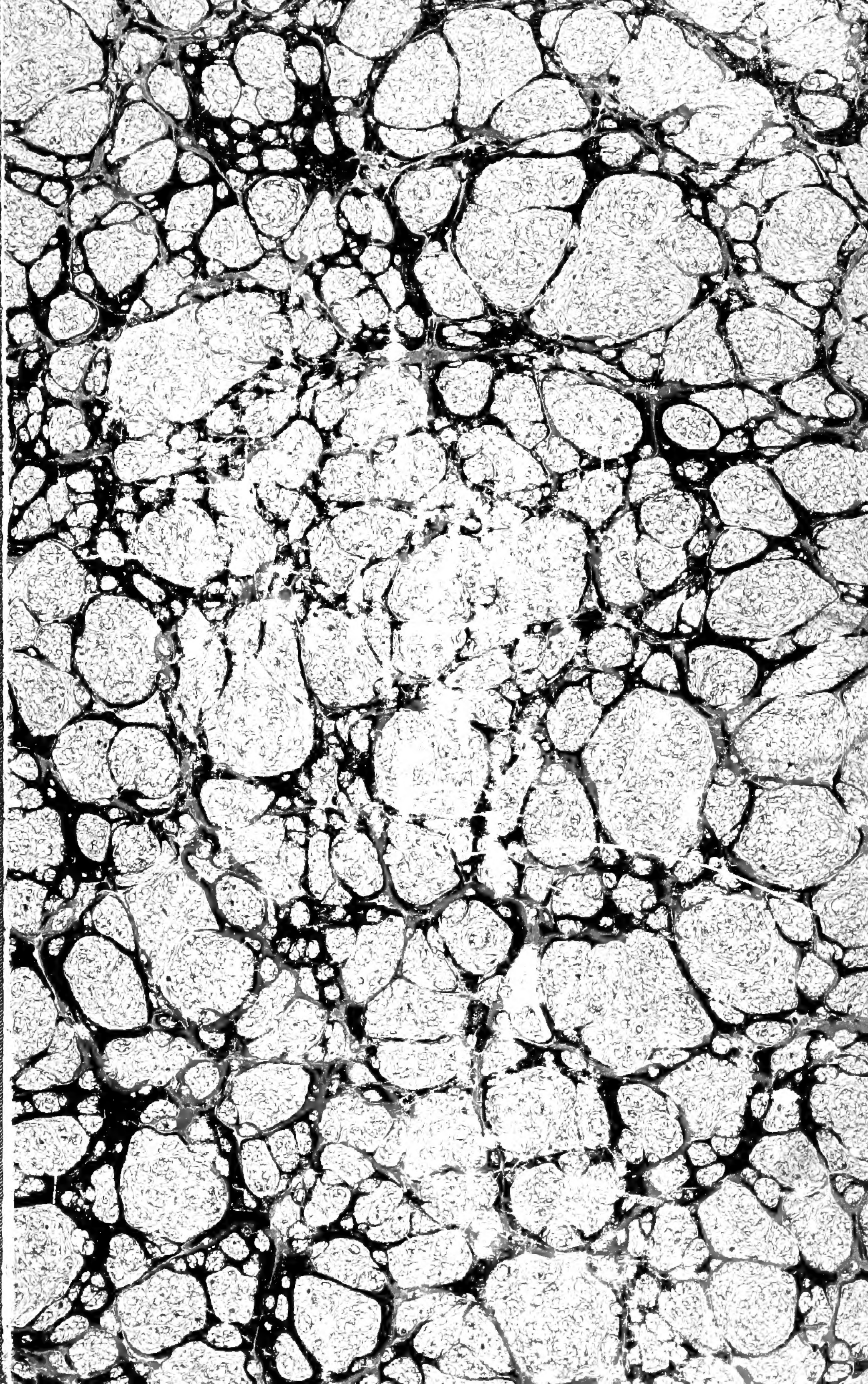

EVOLUTION,

RACIAL AND HABITUDINAL.

BY

REV. JOHN T. GULICK.

WASHINGTON, D. C.:
PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON.
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PREFACE.

In the present volume I have brought together in one connected presentation the chief results of my investigations concerning the factors of organic evolution. Portions of my theory of divergence which were published in the Linnean Society's Journal are reproduced in the Appendix, with careful revision; but the fullest exposition of the fact that all evolution, as we now observe it, is divergent, and that other factors besides natural selection are absolutely necessary both for the origin and the continuance of this divergence, is given in the new chapters constituting the body of the volume. These chapters have been written while considering the most recent biological investigations bearing on the general theory of segregation.

The first four chapters of the volume are introductory, in that they present many facts of divergence and distribution in both natural and domestic species, which remain complete enigmas till the forms of racial and habitudinal segregation have been fully recognized. Chapters V, VI, and VII present the fundamental laws of segregation, and the interaction between the different classes of factors—between isolation and selection, between racial segregation and habitudinal segregation, between autonomic factors and heteronomic factors. In Chapter VI, § II, 14–17 (pp. 101–111), will be found a fuller exposition than has been presented in any of my essays published by the Linnean Society, of the tendency of certain combinations of partially segregative endowments to become more intense in successive generations. It is shown that this is especially the case when endowments, tending toward the mating of like forms with each other, are reinforced by varying degrees of mutual infertility and incompatibility between unlike forms. Appendix II, § IV, 3 (pp. 241–243), briefly indicates several methods of constructing what I have called the permutation triangle. It was first constructed in order to show that the sterility of cross-unions between divergent forms (whether they be varieties, species, genera, or higher groups), would lead rapidly to the extinction of most of these forms, if instincts and other endowments did not facilitate the union of compatible forms. The table thus constructed is found to be a concise presentation of certain classes of probabilities that arise in the pairing of things by chance.

The principles molding segregation, and so controlling variation and heredity, and the effects on racial and social evolution produced by such control, are presented with considerable fullness of illustration on the biological side. For my purpose it did not seem necessary to dwell at equal length on the social aspects.

Another broad department of the subject is referred to in only the briefest way. This is the effect of *amalgamation* or *regressive segregation*, both racial and social. I have, however, pointed out that in the history of man segregation was the leading factor through countless generations when races, languages, and institutions were becoming increasingly subdivided; and that it is only in modern times that the barriers to free intercourse have been so rapidly yielding that regressive segregation has been the predominant feature in human history.

I have presented evidence that, even in the case of invertebrate animals, members of the same species, exposed to the same environment in isolated groups, will often arrive at divergent methods of dealing with the environment, and so subject themselves to divergent forms of selection. If my contention is in accord with the facts, the assumption which we often meet that change in the organism is controlled in all its details by change in the environment, and that, therefore, human progress is ruled by an external fate, is certainly contrary to fact.

It is of no little interest that the recent developments of biological science, in both Europe and America, are pointing, not only to the power of the organism to deal with the *same* environment in different ways, and so to determine the forms of what I have called *active* (or *endonomic*) *selection*, but also the power of many animals to deal with *sudden changes* in the environment in such a way that the group is saved from extinction till "*coincident variations*" have time to arise, insuring completer adaptation to the new conditions through selection. The teachings of biology are thus coming more nearly into accord with that school of sociology which has for years maintained that the social group may learn to determine the form of its own social evolution. We are thus led to hope that man will in time determine his own evolution, racial as well as social; for when sufficiently advanced to realize the breadth of the responsibilities resting upon him, the form of his racial inheritance will naturally be determined by the ideals shaping his social organization.

In the third chapter, and again near the end of the last chapter, attention is called to the fact that, in accommodational and anticipatory action, and in coöperation for the attainment of future results, all forms of life, from the earliest protozoa till we reach the highest types of spiritual life in man, present activities entirely unknown in the inorganic world. In the degrees of attainment reached in coöperative action (with the division of labor and community of interest), and in anticipatory and discriminative action (securing adaptation to future conditions), we find a definite test of the stages of evolution reached—a test that is applicable to the lowest as well as to the highest living creatures.

Of my papers previously published, the one on Divergent Evolution has received the most attention. This is perhaps due to the fact that it was not only published in London in the Linnean Society's Journal for 1887, but was reproduced in this country in the report of the Smithsonian Institution for 1891. I wish, however, to emphasize the importance of the factors enumerated and illustrated in the one on intensive segregation (see Appendix II). If we would fully comprehend the factors producing the segregation of organic types, we must recognize not only the forms of isolation by which groups are first set apart; but also the physiological and psychological forms of segregation by which the slightly divergent forms are held permanently apart, and still further, the factors producing divergence in these isolated groups, and so resulting in intensive segregation. I show that intensive segregation is due not only to the exposure of isolated groups to different environments, but also to the different methods of dealing with the same environment adopted by the isolated groups. I also point out other factors that are subject to change without any change in the activities lying outside of the species; and all such I class as autonomic factors. Throughout all the chapters the underlying purpose has been the investigation of the autonomic as well as the heteronomic factors controlling evolution.

The chief hindrance to the increase of our knowledge of the method of evolution is the tendency to regard some one of the several principles influencing segregation as the one principle controlling the whole process. I believe Prof. H. F. Osborn makes no mistake when he suggests that the ruling method of the next important advance in the interpretation of evolution must be one recognizing the complex action of diverse principles, and at the same time grasping the underlying unity of the process. In the present volume the question is raised whether segregation, with its controlling influence in the spheres of both racial and habitudinal evolution, is not the underlying principle we are seeking. It must, however, be carefully noted that segregation as defined in this volume covers a much wider sphere than isolation. In order to reach the more pronounced results of racial segregation, the separate groups produced by isolation must for several generations be subjected to divergent forms of selection; and in all the forms of animal life that are capable of learning by experience, accommodation, controlled by the principles producing habitudinal segregation, is constantly guiding and shaping racial segregation.

Though more familiar words have been chosen for the title of this volume, the subject here treated would have been clearly expressed if the title had read: "Habitudinal and Racial Segregation; or, the origin and intensification of organic types, guided by innovation and tradition acting under segregate association, and established by variation and heredity acting under segregate intergeneration."

JOHN T. GULICK.

OBERLIN, OHIO.

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[Published in "Nature," April 10, May 8, and August 14, 1890, and April 1, 1897.]

EVOLUTION, RACIAL AND HABITUDINAL, CONTROLLED BY SEGREGATION.

By Rev. JOHN THOMAS GULICK.

CHAPTER I.

INTRODUCTION.

I. FACTS CALLING FOR EXPLANATION.

When a number of closely related varieties and species, occupying adjoining districts of very limited extent, come under observation, the problems connected with the origin of species are liable to be forced upon us. It was therefore natural that when, in 1851 and 1852, I was engaged in collecting the extremely local species of snails found on the island of Oahu, my mind was often occupied with these questions. I observed that each large section of the world had its own peculiar forms of life, and it seemed reasonable to assume that the center of creation for each form had, in most cases, been within the district where it is now found. The most wonderful limitation in the areas of distribution for each species, and accordingly the most remarkable localization of the center of creation for each, was, however, found in the case of the many species of snails living on the trees of the mountain forests of Hawaii. Each valley seemed to be inhabited by peculiar forms. Valleys only a mile apart were occupied by distinct varieties, and often by different species. Groves of candle-nut tree (*Aleurites triloba*), occupying valleys 5 and 6 miles apart, were found to be the homes of completely separate sets of species of snails. I had found not simply a large section of the world within which peculiar species had originated, but ascending a certain mountain ridge a few miles from Honolulu, and looking down, I could say, "That valley to the right, a couple of miles in length and half a mile in width, is the birthplace of the *Achatinella producta* and *Achatinella adusta;* and within the groves of this valley upon which we look on our left were created *Achatinella stewartii* and *Achatinella johnsonii;* while behind us a mile to the northeast, in the jungle that clings to the almost precipitous cliffs on the other side of the backbone of the island, is the secret home of the very rare and beautiful *Achatinella versipellis*."*

My mind was constantly seeking an answer as to why many of the species of these Hawaiian genera of snails should have an area of distribution not more than a mile or two in length, while, in the case of some species of terrestrial mollusks in other parts of the world, the district occupied is a thousand miles or more in length. Again, of Hawaiian species, why should those living continuously in the trees, without descending to the ground even for breeding, occupy on the average areas much smaller than those occupied by species living continuously on the ground?

The mystery was only intensified when I observed a certain correlation between the form of the island on which the species had originated and the method of grouping and distribution of the species and varieties. In the first place, the forest species on one island are never completely intergraded with those on another island. Again, the intergrading of nearly allied species on one island usually relates to species found in contiguous valleys; while the most divergent forms are found in the districts that are most widely separated. On West Maui, which is a single conical mountain, deeply furrowed with valleys and gorges radiating from one center, we find each group of species lying in a circle around the mountain, each species occupying its own district, though intergrading with those of adjoining districts, and no one of the species strongly divergent from any of the others of the same group—a distribution that seemed symmetrical and impressed me as strikingly similar to the distribution of groups of birds and mammals around the North Pole; for example, the distribution of species of bears throughout the Northern Hemisphere. But, in strong contrast with this, is the distribution of species of snails on the island of Oahu. Here the forest region, in which the snails are mostly found, is not spread in a circular form over a group of radiating valleys, but lies in a strip about 35 miles in length and from 2 to 6 miles in width, upon a mountain range; and the forms of one closely related group are distributed in two parallel series of species on opposite sides of the ridge, the most divergent forms being those

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* In Plate II, figs. 11–25, are given 15 species of Achatinella, distributed in the groves of five valleys, and, therefore, limited to an area less than 5 miles in length and not more than 2 miles in width. Of these 15 species there are nearly a hundred easily distinguished varieties. Moreover, several other much rarer forms of Achatinella found on the vegetation of the same district have been described as separate species; and of 6 other genera of the family Achatinellidæ there are, within the same limits, 17 or 18 strongly marked species.

that are separated by the greatest distance, which also corresponds with separation by the greatest number of valleys and mountain spurs.

I had read Darwin's account of the Galapagos Islands given in "The Voyage of the Beagle," and had noted the astonishment with which he had discovered that islands within sight of each other were the homes of closely related but diverse species—a marvel which he in no way attempted to explain; and here, in the snails of Hawaii, I had found differences more wonderful, for each valley of the same island was the home of peculiar forms. When Darwin's "Origin of Species" appeared in 1859 I read it with intense interest and with complete assent to his argument that large groups of widely divergent species had been derived from common ancestry; but the more I meditated on the scope of natural and sexual selection as factors producing transformation, the more clearly I perceived that they were not adequate to explain the diversity of these species exposed to the same external conditions; neither did they afford any explanation of why the areas of distribution for many of these species are so extremely limited, while some species of terrestrial mollusks are distributed over vast areas.

II. FACTS SHOWING THAT IN THE CASE OF MANY DIVERGENT SPECIES DIVERSITY OF NATURAL AND SEXUAL SELECTION IS EITHER WANTING OR, IF PRESENT, IS THE EFFECT AND NOT THE CAUSE OF THE DIVERGENCE.*

1. *In Many Cases of Divergence Diversity of Sexual Selection can not be the Cause.*

In the case of mollusks, the diversity in colors and forms presented by closely allied varieties and species can not be attributed to diversity in the direct action of the sexual instincts of the different groups, by which those of certain forms and colors are allowed to mate, to the exclusion of all other forms and colors; for there is no reason to believe that differences of form and color are capable of being at all observed by the senses with which they are endowed. Even in the case of highly endowed animals, where diversity in the styles of ornamentation desired in mates, and therefore diversity in the forms of sexual selection in closely allied varieties and species, may be readily granted, the problem of chief interest is not concerning the effect of these divergent instincts, but rather concerning the causes by which they have been produced; for why should an isolated section of a species possess instincts in any degree differing from the instincts of the main body of the species? Sexual selection is, therefore, an in-

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* In Chapter IV will be found illustrations of divergence under the same environment.

complete explanation of divergence, even for higher animals; and in the case of creatures as low as mollusks it would seem to be entirely excluded from having any effect in determining the diversity of color in the different species.

2. *In Many of the Same Cases Diversity of Natural Selection can not be the Cause.*

First. *Because in many cases divergence is not in proportion to the degree of difference in the environments surrounding the separated varieties and species.* This is true not only in regard to the divergence of genera and subgenera of snails, occupying different islands of the Hawaiian group, but in regard to the divergence of the varieties and species of the same subgenus, occupying the different districts of the same island. Darwin's theory assumes that when a few members of a species form a colony in a new district divergence is produced only when, and in proportion as, the new district presents conditions unlike those found in the original habitat of the species. This interpretation fails to explain the origin of the species we are now considering. For example, valleys separated by narrow mountain spurs, on the southwest side of the main mountain range of the island of Oahu, are exposed to similar wind, rain, and temperature; the soil has come from the disintegration of volcanic rock, without limestone; the vegetation on the ridges differs from that in the valleys; but in most of the valleys we find groves of candlenut trees (*Aleurites triloba*), and clinging to the trunks and branches of the trees in these groves in any one valley we find several species and many varieties that are not exactly reproduced in any valley more than 2 or 3 miles distant. The valleys of Manoa and Nuuanu are but 3 miles apart, but they present a greater difference in vegetation than that found between Manoa and Kawailoa, which are 20 miles apart; the divergence in species of Achatinella occupying these valleys is, however, much less in the former case than in the latter. This is the reverse of what we should find if the divergence were due to exposure to unlike conditions. This is not an exceptional case. The land mollusks of the Hawaiian Islands present a vast body of facts of this kind.

Second. *Because in some cases the divergence is in non-utilitarian characters.* If these snails were endowed with powers of vision and discriminating instincts as highly developed as those of birds, it might be argued that the brilliant colors characterizing certain species were developed by what I have called social segregation, with the aid of sexual and social selection, including the need of recognition marks, which Mr. Wallace has pointed out as a prime necessity in the segregation of higher animals; but, as we have no reason to think that they possess the power of discriminating colors, we must seek some other explanation. If the colors were of a protective character we might surmise that they had been developed through exposure for many generations to sharp-sighted enemies; but in the case of many of the species, their white and green tints striped with black make them conspicuous objects against the brown trunks of the trees on which they are constantly found. Neither are their colors for warning; for these snails are not repulsive to flesh-eating birds. It is, therefore, hard to avoid the thought that these striking colors are of no service in protecting the life, either of the individual or of the species. Again, certain birds of prey are the only aboriginal creatures that could be suspected of feeding on these snails; and as the birds have a wide range, the immense diversity of color in the snail shells of one island would remain unexplained.

There is, also, another character in which species of some of these genera often differ from each other, in regard to which natural selection has never been shown to be the controlling factor. I refer to the character of the coil of the shell, which may be dextral in one species, sinistral in another, and either dextral or sinistral in a third. As long as it is impossible to give any reason why a species would not be equally successful if every individual possessed the reverse form from that it now has, it is unreasonable that we should attribute the present form to the influence of natural selection.

The theory that there is great advantage for the species in having all the individuals coiled in the same way, if proved, would in no way explain why certain species are always dextral and certain others are always sinistral, while some well-established species present large masses of individuals of each form. I think it will some day be shown that snails of opposite forms, though of the same race, are incapable of mating with each other, and we already know that each individual is both male and female. If, then, an unusual sport should produce, in the same family, or on the same tree, two individuals of the reverse form from their parents, we should have a completely segregated variety established in the original home, while exposed to the same environment and using it in the same way, and its new character conferring no benefit.

Third. *Because in the case of certain divergent species of Achatinella, occupying isolated valleys presenting the same vegetation, the diversity of selection to which they are subjected through different habits of feeding is directly preserved by the isolation which prevents the peculiar habits from being broken down by free crossing.* The habits of feeding are not without variation even in the original valley. When, therefore, one or two individuals with a special habit of feeding are transported to a new valley, it is not at all strange that they choose to pass by some plants used by many varieties of the species in the original home. Moreover, their descendants may never regain the power to feed on as many kinds of plants; or, if on as many, probably not on the same kinds. Still further, when a distant valley has been reached, after a number of such transfers, each transfer being followed by a long history of habit building, without the influence of crossing with individuals of the original stock, is it at all strange that the habits have become widely divergent, and that they are the cause of divergent selection tending to establish the divergent habits in a more fixed form?

In such a case as the one just described the new habit and the diversity of selection, with the diversity in the direct influence of the environment, can not be ascribed to any advantage over the old form resulting from the new habit; for competition with the old form has ceased for countless generations. Moreover, if the later history of the newer species has been in a new and unoccupied district, competition with all allied forms has ceased; and the new habit is simply one of several forms of using the environment that are open to a new colony, unaffected by constant crossing with the old stock.

III. May not the Prevention of Free Crossing be an Explanation?

It will probably have already occurred to many of my readers that the wonderful limitation in the areas of distribution occupied by the separate species of Hawaiian snails is in some way connected with lack of powers and opportunities for migration; and now as we reflect that the same lack of migration would immeasurably increase the isolating effect of some rare occurrence by which a single individual is carried a mile or two beyond the home of the species, into a region of abundant food, the question naturally arises whether the isolation, which prevents all chance of crossing with the original stock, does not open the way for new habits, for new forms of selection, and accordingly for the transformation of the new colony into a new variety, and finally into a new species.

We have here reached the idea of freedom from crossing with the old stock, or isolation, in the broader meaning which has been given to the term by writers on evolution since the days of Darwin. I believe that no process of natural selection, or of sexual selection, or of any other form of selection, can transform one species into two or more species without the prevention of free crossing between the branches that are thus transformed. Isolation is, I believe, an essential factor in the production and maintenance of divergent types, whether they be varieties or species; and any theory that fails to consider the causes and effects of isolation is an insufficient explanation of divergent evolution. Still further, as the general trend of all evolution is toward increasing divergence, the influence of isolation is fundamental in all the processes of organic evolution.

IV. Investigation of the Causes and Effects of Segregation.

The purpose of this volume is to investigate the causes and effects of what I have called "segregate breeding," or simply "segregation." Segregation is the intergeneration of like with like, with the prevention of crossing between unlike groups. I maintain that segregation ranks as one of the fundamental principles controlling the relations of organic beings to each other. Moreover, in the processes of organic evolution, the principles controlling the modification of segregation are the principles that control the variation and heredity. It is only as it aids in producing and intensifying segregation that any form of selection becomes effective in the evolution of organic types. I maintain that the inheritance of acquired characters is not yet fully proved or disproved; but if future investigation should show that the special training of parents for several generations results in the transmission to offspring of modified innate endowments, there could be no doubt that to gain the full effect of such training on offspring there must not be free crossing between the trained and the untrained. Segregation, even under such conditions, remains a leading factor, and modification of segregation will, I believe, be found to be the principle controlling the evolution.

Lamarck recognized that distinct organic types could not be maintained without some form of isolation;* and such Neo-Lamarckians as Professor Packard have been even more emphatic in placing this principle among the essential conditions for divergent evolution.†

V. Segregation the Unifying Principle in the Complex Process of Evolution.

If heredity is a fundamental power, then segregate breeding must be a fundamental principle in the formation, continuance, and control of divergent types; for diversity of type is diversity of inheritance, and diversity of inheritance can not be initiated or maintained where

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* "Lamarck, His Life and Work," by A. S. Packard. New York and London. Longmans, Green & Co. pp. 319, 320.

† *Ibid.*, pp. 392–396 and 404–406.

there is a free blending of the different types of inheritance. Now, it is recognized by all that the influence of the different forms of selection rests on heredity; if, therefore, we so expound natural selection as to deny the fundamental laws of heredity expressed in the dependence of divergence on segregate breeding, we undermine the foundations on which the importance of selection rests. Clear recognition of the laws of life makes it plain that a consistent theory of divergent evolution can not be constructed without considering the principles by which segregate breeding is modified and intensified. Those who trace these principles, and who show that diversity of natural selection and the other forms of selection are effective in producing divergent types only when coöperating with isolation in producing segregate breeding, are simply recognizing the unfailing influence of heredity. Segregation is the fundamental process to which all the principles helping to produce divergent evolution must contribute.

I consider it important to recognize the very different spheres filled by the principles of selection and isolation, and to so define the terms that they do not overlap. But I also maintain that there is a correlation in the two processes, in that both coöperate in controlling heredity and variation, and so in producing ever-increasing segregation of organic types. The fundamental unity of the processes producing evolution, whether these processes are originated and controlled by innate powers or by acquired characters, and whether these powers maintain relations with other members of the species or with conditions external to the species, is found in the fact that they all coöperate in producing segregation.

CHAPTER II.

BIONOMIC LAWS.

I. BIONOMIC LAWS AND THE METHOD OF THEIR INVESTIGATION.

1. *Bionomics and Its Scope.*

The organic world as we find it consists of many groups of individuals, each group, with but few exceptions, being propagated by the union of male and female elements produced by parents belonging to the same group;* while the elements of different groups are either incapable of fruitful union or in nature seldom have an opportunity for such union. Each group possesses characters of its own, distinguishing it from all other groups; and these characters are inherited by each successive generation of the group, except in cases known as alternating generations, in which the persistence of character is revealed in a series of two or more generations that return to the original form. These persistent groups which are prevented from crossing by the incompatibility of their sexual elements or by some other form of segregation are usually called species; but when the difference of character is slight they are often called varieties; and when the differences are not easily recognized they are not even regarded as different varieties. Each persistent group differing more or less from every other group, and reproducing its own form without commingling with other forms, I call a type.

The doctrine of evolution teaches that the vast multitude of organic types now inhabiting the world are the descendants of but few and perhaps of but one original type. Bionomics is the science that treats of the origin of organic types and of the relations in which they stand to each other and to the physical environment.† In this volume some of the fundamental laws of bionomics will be considered.

2. *Why we Commence with the Method of Evolution without first proving the Fact of Evolution.*

It may be thought by some of my readers that before discussing the laws of evolution logical method would demand that I should consider

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* Examples of these exceptions are found in plants that propagate by shoots or bulbs without ever producing seed, such as banana; also in parthenogenetic plants and animals.

† Prof. E. Ray Lankester has proposed this use of the word "bionomics" in the article on Zoölogy, in Encyc. Brit., 9th ed.

whether the evolution of species is anything more than a doubtful hypothesis. In other words, it may be thought that the attempt to explain the method of evolution before it has been proved that there is such a process is an inversion of logical method. Further consideration will, however, show that the greatest obstacle to the general acceptance of the theory of evolution has been the difficulty in believing that this wonderful transformation is being wrought out in our very presence, and that the laws in accordance with which it progresses are in a large degree open to investigation.

The possibility of recognizing this stupendous reality has been shut out of the mind by the double assumption that the methods of creation are necessarily inscrutable and that the process of creation has been closed never to be reopened. As both these assumptions are without proof, the shortest method of setting them aside is to show that the energies of creation are ever working in the ordinary processes of life. The effectiveness of this general method of appeal to actual experience and observation is seen in Darwin's "Origin of Species." He there first shows that a process of breeding, which in domestication always results in divergent varieties, is also being carried on by natural causes. He then shows that if we assume that species have been produced, one from another, by some such process, the relations of species to species, not only in the groups of scientific classification, but also in their geographical distribution over the earth and in their geological successions in time, become intelligible, and present a network of interrelated and significant phenomena, the causes of which can be more or less fully traced. I propose to follow the same general method. But as present debate relates to the principles and causes on which evolution depends rather than to the proof that such evolution has taken place, I shall give my chief attention to the first part of the argument. I shall discuss the forms and laws of bionomic action by which the relations of species to species are being maintained or modified, and shall refer to the results of this action as revealing the nature of the process.

3. *Need of Investigation of all the Forms of Interaction causing Transformation.*

Inquiries leading to the discovery of bionomic laws have usually been first suggested by observing the relations under which organisms present themselves as distributed in nature; but after we have once recognized the fact that these relations are the result of the constant interaction between organism and organism, and between the organism and the physical environment, it becomes necessary to make a full classification of the different forms of interaction that tend to modify the species. A systematic and thorough use of this method will, I am convinced, throw light on many problems, correcting many partial and incomplete theories. We may also hope that a careful examination of the different forms of interaction will, in some degree, lessen the danger of attributing exclusively to one form of interaction results that are really due to several forms. And having discovered that similar results are produced by different forms of action, we are next led to seek for the underlying principle in which they agree.

4. *Natural and Sexual Selection not the only Factors producing Transformation.*

The relation of the species found in any one of the Galapagos Islands to those found on other islands of the same archipelago, and, still further, their relation to the species in South America, suggested to Darwin the idea that they had arisen through the modification of South American species. This idea he elaborated, supplementing and supporting it by attributing the transformation of species to two chief causes—natural and sexual selection. That these two factors must be effective in producing permanent transformation was argued from the effect of artificial selection in producing divergent races of domestic plants and animals, and from the observed fact that in many cases natural varieties and species present degrees of divergence corresponding to the time during which they must have been exposed to different environments. These principles have thrown a flood of light on differences between the sexes of the same species, and on those differences of species by which they are adapted to their different environments; but do they show that there can be no divergence in the isolated portions of a species exposed to the same environment, or that all the divergences that arise in portions exposed to different environments are adaptations to the environment? Are all the diversities of sexual selection by which different portions of a species are differently modified due to differences in the environments of these portions? If not, we have a cause of divergence that does not depend on exposure to different environments. Moreover, if we assume, as most do, that the differences in sexual selection in the separate portions of a species are due to differences in the sexual instincts of the portions, the question arises as to how we are to explain the divergence in the sexual instincts of individuals exposed to the same environment. Is it not apparent that in the facts brought forward for the proof of this principle of transformation other principles are involved?

Further observation brings to light many cases in which separated portions of a species have adopted different industrial habits, while exposed to the same set of conditions, the diversity in the forms of selection by which they are molded being due to the different uses they have made of the same resources, and not to any difference in the resources found in the different districts.

As these facts will be presented in detail when discussing the principles upon which I believe they depend, I need not dwell upon them here. It is sufficient for our present purpose to show that the problems of divergence are not fully explained by natural and sexual selection.

5. *Comparison of the Conditions to which Natural Species are Exposed with the Conditions producing Domestic Varieties.*

Believing that other principles besides natural and sexual selection must be effective in the production of specific differences, I propose to make systematic search for them in the interactions between the members of the same species and between the species and the environment. Following the example of Darwin and Wallace, I shall seek suggestions for the guidance of my search from the experience of the breeder of artificial races. In the maxims and traditions of those who are engaged in raising highly prized varieties of plants and animals, we have the treasured results of thousands of years of experiment in biology. In these results we shall, I think, find principles that have not been fully considered in the problems of evolution. This method of presenting the subject I adopt as best suited for exhibiting the relations in which the different laws stand to each other, but I would not wish to have anyone suppose that it represents the order of the steps by which these laws were first reached and by which their relations to the origin and transformation of species were first recognized. The problems requiring solution were in every case forced upon my attention, not by the study of domestic races, but by observing the conditions under which divergence has arisen between natural varieties and species. Having discovered that in nature many divergencies appear in varieties and closely allied species exposed to the same environment, and sometimes in those using the environment in the same way, I concluded that natural selection could not be the essential and fundamental factor in the multiplication of species. I then turned to the production of domestic races, and found, on the one hand, that artificial selection could avail nothing in producing divergent forms, unless it was aided by isolation, and, on the other hand, that isolation, if not producing divergence from the first, was sure, when long continued, to end in divergence, either through diversity in the habits determining the use of resources or through some other principle producing transformation of the isolated portion of the species. These conclusions, gathered from the experience of the breeder, were then applied to the explanation of the phenomena of divergence as appearing in nature, and any residual phenomena not at first explained were again brought to the test of experiment as revealed in the experience of the breeder. The process of discovery is often very intricate, while that of exposition and proof is comparatively simple and direct; and it is not surprising that this has been found to be especially true in the case of the laws governing the complex relations determining the evolution of species.

II. The Production of Domestic Races.

Six subjects must be considered. In studying the production of domestic races we need to take up separately the different results reached, with the methods by which each result is realized, and the conditions that are necessary for success. We shall consider: (1) the conditions on which the continuance of the race or species depends; (2) the process by which a race possessing certain characters is transformed into a race possessing different characters; (3) the process by which one race is transformed into several races; (4) the process by which the stability of a new breed is established; (5) the process by which divergent races are amalgamated and commingled; and (6) the influence of acquired characters on racial characters.

1. *The Continuance of Races.*

In the domestication of any species one of the first questions is, Can food or other needed resources for maintaining its life be furnished under domestication; and if so, has it adaptations to the wants of man such as to induce him to furnish the needed maintenance? If this double question can be answered in the affirmative, the probability of its being domesticated will turn on its retaining its power of propagating when brought under the new conditions. The elephant, though a useful animal, has failed of developing a domestic race through failing to propagate with any certainty under domestication. The preservation of a domestic race depends on its securing maintenance through adaptation to the rational environment, just as the propagation of a species under nature depends on its securing maintenance through adaptation to the natural environment; and if either the race or the species is to survive there must be such coordination between sex and sex, and between the sexual elements of the group, as will secure impregnation, and the production of both male and female elements must be sufficient to prevent extinction.

2. *The Transformation of Races.*

The survival of a race or species depends on its having sufficient adaptation to the environment to secure maintenance, on there being sufficient compatibility between the sexes to secure fertility, and on the production of male and female elements in sufficient abundance to secure fecundity; but the presence of these conditions does not insure the transformation of the race or species enjoying these conditions, nor does the extinction of races or species lacking in these conditions insure transformation in the surviving forms. As domestication prevents or greatly impairs reproduction in the elephant, this species does not survive under domestication and therefore escapes the transformation necessary to produce a domestic race. For a similar reason, the complete extermination of the American bison would not produce a new race of bisons; and it could have influence in transforming an associated species of some other family only in case the absence of the bison should introduce a change in the relative degrees of maintenance, compatibility, or fecundity possessed by the different variations of the species, so that the most successful should be other than those that were most successful during the period of association with the bison. A little reflection will reveal the fact that when the change of relative degrees of maintenance or fecundity pertains to races or species which are entirely prevented from crossing the relative numbers in which these groups exist will be changed, but that this will not be a cause of change in the characteristics of the groups, even if some of them become extinct. This will be distinctly seen if we take a definite case. For example, during one year turkeys may attract the attention of a poulterer, and the next year peafowls may become his favorites; but the change in the relative importance given to either species transforms neither the one or the other. Again, he may have a pair of a species which he would gladly multiply, but through difficulty in getting them to mate his success may be very limited; or in the case of a second desirable species that pairs freely, diminished fecundity may interfere with their multiplication, while at the same time a third species of no great value, but not limited by these disabilities, multiplies freely and is raised in large numbers. The point to be observed is that in all these cases the difference in the degrees of propagation of these different species is not a cause of transformation in the characteristics of the species.

Neither change in the relative numbers in which we choose to raise two species, nor diversity of success in raising those that are equally desired, can be the cause of transformation of species, as long as the proportions in the variations of the intergenerating forms of each species remain unchanged. Diminution and extinction on the one hand, or increase and unprecedented multiplication on the other, are alike without effect in changing the character of a race, or a species, as long as the proportionate propagation of the different intergenerating forms or variations that constitute the race or species remains unchanged.

In other words, the selection that produces transformation is not the selection of one segregated race or species to the exclusion of another, but the selection, from the offspring of one intergenerating race, of certain forms that do not represent the average character of the race, and giving to them either exaggerated or exclusive opportunity to propagate the race. Failure to recognize this distinction has been a source of confusion in the reasoning of certain writers on evolution.

Briefly stated, the process on which breeders chiefly rely for transforming a domestic race, without dividing it into divergent races, is unbalanced propagation through exclusive breeding from individuals whose average endowment, in some chosen character, is above the average endowment of the whole race. This is often secured by destroying the least acceptable individuals before they propagate. Of the American bison there are supposed to be about 600 surviving individuals. If these were all brought together in one park, and if in each successive generation all those that ranked above the average of their generation in length of horns were slaughtered before they came to maturity, there can be no doubt that after many generations the whole species would be transformed into one possessing shorter horns than those that now characterize the species.

This process would be one method of securing what is usually called selection in the breeding of animals; and selection is regarded as the chief means by which the different races of domestic animals have been produced. It should, however, be noted that the success of this process of transforming the species depends on certain conditions that are not secured by the process of selecting. It is necessary that there should be in each generation such a difference in the length of the horns that it is possible to tell with certainty which are above and which below the average. Again, there must be such a degree of fertility and such success in attaining maturity that there shall be a considerable surplus of individuals of both sexes that may be slaughtered without gradually exterminating the race. Again, it should be observed that it is not every kind of selection that produces transformation. It is only as selection results in the preservation of other than average forms that it has any influence in transforming a race. The selection of average forms for propagation tends to produce stability of type; and the selection of extreme, but of opposite, and, therefore, balanced deviation from the type produces fluctuating variation; but unbalanced selection, that is, propagation from forms whose average character differs from the average character of the race, changes in some degree the average character of the race in the next generation. Whenever this takes place, whether it be by the design of man or not, there transformation takes place.

Unbalanced artificial selection is not the only principle producing the unbalanced propagation of the variations of domestic races. Unbalanced natural selection caused by change in climate or in other external conditions, and resulting in the superior success of other than average forms, will also produce unbalanced propagation of domestic as well as of wild races. Again, it may be that some form of variation that is above the average in strength or skill, or in the length of natural weapons, or in the beauty of its adornments, will gain an advantage over its fellows in the appropriation of food or in winning mates, and so become subject to some form of reflexive selection, by which unbalanced propagation is produced.

There may also arise unbalanced elimination, when, through some overwhelming catastrophe, a large portion of the domestic stock is destroyed, and the remaining individuals that propagate do not represent the average characteristics of the race. This may be called indiscriminate elimination. Indiscriminate elimination arises when war, famine, pestilence, or earthquake falling upon a tribe of men results in the indiscriminate destruction of nearly all of their domestic animals; and in many of these cases the surviving individuals from which the stock is afterward propagated do not represent the average character of the previous stock.

Again, some variation of the stock may be endowed with a degree of fecundity decidedly above the average fecundity of the rest of the stock; and, if the form possessing this superior fecundity is as well adapted as other forms to meet the desires of those who raise the creatures, unbalanced propagation will take place, and the average character of the stock will be changed. In my paper on Intensive Segregation* I call this principle fecundal transformation. Karl Pearson has discussed this principle under the title of "reproductive

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* See Appendix II.

selection," in a very interesting chapter of his volume entitled "The Chances of Death and Other Studies in Evolution." I fully agree with this author in the emphasis he puts on the importance of a careful statistical investigation of the subject; but I think the term he has chosen would naturally apply to sexual and impregnational selection as well as to this form of selection which is dependent on degrees of fertility. If these are all to be called forms of selection, I would suggest that the special principle under consideration might be designated fecundal selection, and its effect on the group might be called fecundal transformation.

3. *The Divergence of Races.*

In order to produce two or more divergent breeds from one breed, it is necessary, first, that the original stock should be divided into separate portions that are prevented from crossing (this is conveniently called isolation); and, second, that there should be some cause transforming one or more of these separated portions. Now, the cause producing transformation in a separated portion may be the incapacity of a given small fragment of a race or species to perpetuate the original average character of that race or species; or, after separation, the portion may be subjected to some form of unbalanced selection.

Returning, for illustration, to the 600 bison, we may suppose them to be indiscriminately divided into two isolated herds of 300 each, in which case the average character of each herd would probably be nearly the same as that of the other herd, and the descendants of the two herds, if not subjected to different kinds of selection, would probably present no important differences, at least for many generations. If, however, the whole herd were broken up into pairs, the offspring of the pairs forming 300 isolated groups, each of which was never allowed to cross with any other group, we should probably find that perceptible divergences would soon present themselves in some of the groups, even if they were not subjected to unlike selection.

Another form of isolation, still more effective in producing divergence, would be gained if the individuals presenting the highest degree of some special kind of variation were brought together in one group that was prevented from crossing with the others. The division of organisms which have descended from one original intergenerating group into two or more groups that do not possess the same average character, and that lack either the capacity, inclination, or opportunity for intergenerating, I call segregation. Whenever there is a closer resemblance between the members of an intergenerating group than between them and the members of some other group with which free crossing has been interrupted, there segregate breeding or segregation exists. If it were possible to divide the 600 bison into two completely equivalent groups, the isolation of these two groups would not involve segregation; but the indiscriminate division of any intergenerating group into two or more isolated groups usually involves more or less difference in the groups, and, therefore, more or less segregation.

If we carefully consider the process by which the different domestic races of any species have been produced, we shall find that the isolation of each race from every other race has, in every case, been a prime factor. Until modern times the hostility of different tribes of men and the want of free commerce between nations have secured the isolated breeding of the domestic races under the care of different tribes and peoples. Now, according to the principle I have just pointed out, the initial differences between those portions make them more or less segregated groups whenever free crossing between the portions is cut off. But this initial segregation is soon intensified by the transforming influences to which the different portions are subjected. As each portion is subjected to the care of a separate tribe of men who preserve such individuals of the offspring as best suit their purposes or fancies, and as the individuals thus preserved seldom represent the average form of the wild species, transformation is soon produced. Each isolated group, if it survives under its new conditions, must produce forms increasingly adapted to meet the desires of those who care for them; and even when those on whom they depend have no idea of developing new characteristics by selection, unconscious selection usually takes place. If the selected form is not the average form, transformation necessarily follows. But as we are now considering the process by which *divergent* evolution has been produced in domestic races, the important point is, not that transformation is usually produced by domestication, but that, when this cause of transformation modifies continuously isolated portions of the same species, the result is *always divergent* and *not parallel.* Account for it as we may, when a domestic breed has been transformed during isolation, the transformed portions are always found to be more or less unlike; and this is so even when the physical conditions are the same, and when the persons on whom the selection has devolved are representatives of the same race.

I think it will be found that independent transformation (that is, transformation during isolation), is always divergent and never completely parallel; and I believe this to be so whether the transformation is due to unbalanced natural selection or to some other principle, as, for example, the direct effects of use or disuse, or to indiscriminate elimination. Just as indiscriminate isolation may produce unbalanced groups, and, therefore, segregation, so indiscriminate destruction in the isolated groups is liable to produce unbalanced propagation of diverse kinds, and so divergent transformation with intensive segregation. If animosities arise between two sections of a tribe, the domestic animals in the care of the two sections, though completely isolated, may present no apparent differences till famine or some other calamity leads to the indiscriminate slaughter of all but a pair or two of some species in one of those districts. This small fragment will, in many cases, be unable to reproduce in all respects the average character of the original race, and will become quite perceptibly divergent. If heavy but indiscriminate elimination falls upon the representatives of a given species in both sections of the country, the divergence in the isolated groups will be likely to be somewhat greater than if but one section suffers. This principle differs from natural selection in that the exclusion is indiscriminate instead of discriminate. Extreme elimination, leaving only a very small remnant, is always unbalanced elimination as regards some of the characters and, therefore, tends to produce transformation.

Again, the effects of crossing between different strains and races of the same species may occur in different degrees in the different districts over which a species is distributed, and may, therefore, result in divergences in different districts. This principle I have called amalgamational transformation.

4. *The Stability of Races.*

For the preservation of a given race-type it is usually considered necessary to exclude from propagation a certain proportion of the variations that fall below the average which constitutes the type. The degree of exclusive breeding that is needed to maintain the present average depends upon the stability of the type, that is, the weakness of the tendency to revert to forms possessed by more or less remote ancestors. Whether a type may become so fully established as to maintain a constant average without any tendency to reversion, is perhaps an open question; but in the case of the goose, which is one of the most stable of domestic species, it is not certain that what has been called the birth average more closely resembles ancestral types than does the average that comes to maturity and propagates the species. The vitality of those that live and propagate is undoubtedly higher than that of the whole generation; but this does not prove that selection is necessary to maintain the distinctive characters of the species. The effect of cessation of selection is a subject of great interest, on which further light is needed. In dealing with an ordinary species, the breeder assumes that the exclusive propagation of average forms will tend to produce stability of type rather than reversion; and he ignores any difference that may exist between the birth-average and the adult-average. His only hope of producing divergent races is found in the separate breeding of forms that are manifest departures from both the birth-average and the adult-average in some given direction. If sheep with long and fine wool are desired, he selects sheep possessing these qualities in the highest degree as the ones from which to raise his flocks.

5. *The Amalgamation of Races.*

Once more, the breeder finds that the free crossing of different races introduces great variation, with the breaking down of race distinctions. The interfusion of races, with the strange preponderating influence that belongs to some races, or sometimes to one sex of a given race, is a subject that is worthy of fuller study than has yet been given to it.

6. *The Influence of Acquired Characters on Racial Characters.*

Fully satisfactory proof or disproof of the direct inheritance of acquired characters has not yet been accumulated; but as I pointed out in my paper on "Intensive Segregation," reproduced in Appendix II of this volume, their indirect influence on inheritance is certain; for "All diversities of environal selection that do not vary according to differences in the environment must be classed as diversities of active selection (or endonomic selection, as I sometimes call the principle), for they must have originated in some variation of the powers of the organism, *or in the diversity of uses to which it has put its powers.*"* In the same paper I further called attention to the fact that where a group of species possessing extremely limited powers and opportunities for migration are distributed in a district, where all the other species of both plants and animals have the usual powers and opportunities for migration, here we find the group, with limited facilities for migrating, varying, though the environment, both physical and organic, is essentially the same. Observation also teaches us that when a gravid female of a variable species is isolated

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* The small species of Achatinella found in the valleys in the northwestern portion of the island of Oahu have different habits of feeding from those of larger size found near the eastern end of the island. (See Plate II and the explanation of the same, Chapter IV.)

in a region furnishing the same environment as the original home from which it has been transported, some peculiar habit of feeding, acquired in the original home, may become the transmitted habit determining the life of the new colony, and so determine the forms of selection to which the new group is subjected. This form of selection I call active or endonomic selection. Again, there is reason to believe that the different forms of reflexive selection, of which sexual selection is the most familiar example, may gradually change in an isolated portion of a species without depending on change in the environment. In these and other ways I have shown that many groups of organisms are undergoing transformations that can not be attributed to changes in the environment. The subject has been presented in several forms in the paper referred to above, reproduced in Appendix II. As a further illustration of my idea, I would say that I think there is no reason to claim that our arboreal ancestors were forced to forsake the traditions of their fathers, through the failure of the forest to grow, or through any other change in the environment. It is more natural to suppose that the great prosperity of our forebears in the forest regions increased their numbers till it became desirable that some new sphere of activity should be discovered. The rich rewards that came to the more enterprising ones, who searched the open country by day and hid in the caves at night, was probably the beginning of the change that has led to the separate methods of use for our fore limbs and our hind limbs. The great advantage of standing erect and taking a broad look over the fields of deep grass started selection toward human feet. This view of the course of evolution reveals the influence of habit in controlling selection, and so finally in controlling inheritance. The frequent control of the form of survival by the activities in the organism, and not by change of activities in the environment, was emphasized in my papers published by the Linnæan Society; and more recently the importance of individual adjustment to sudden change, through the securing of time for "coincident variation," has been pointed out by Lloyd Morgan* and others.

As the processes mentioned under these six heads, when brought about in domestication, produce, in the first case, either continuance or extermination of the race; in the second, simple transformation; in the third, divergence; in the fourth, increased stability; in the fifth, increased variation with blending of types; and in the sixth, transformation in the organism that does not depend on change in the environment, we have reason to expect that when produced by

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*See "Habit and Instinct," 1896, pp. 312ff.

natural causes the results will be essentially the same. These may all be classed as processes of evolution, that is, processes by which a type is either preserved or more fully established or intensified, or through which it unfolds divergent forms, or through which it is commingled with other types. In the whole process of organic evolution the fundamental activity is the reproduction of individuals, endowed with the double acting quality of variation and heredity, which is constantly controlled and shaped by the more or less rigid realization of the law of segregate breeding, or the intergeneration of like with like with the prevention of crossing between unlike groups. As we have seen in the brief description of the production of domestic races just given, there are several different methods by which unbalanced propagation may be brought about, and wherever unbalanced propagation is produced, there transformation is the result, and there segregate breeding is intensified. Again, there are several methods by which a single intergenerating group may be divided into two or more groups, with free intergeneration within each group, while there is prevention of crossing between the groups; and some form of this process of isolation is an essential condition for divergent evolution; for without isolation, variations of divergent types can not be accumulated. In order to understand the method of evolution, it is necessary to keep in mind the initial segregation produced by the different forms of isolation, and the intensified segregation produced by the different forms of selection and other influences (including diversity of habits), which insure the transformation of the isolated group.

After this brief survey of the causes of divergence in domestic animals, we will now turn our attention to divergent types that have arisen under natural conditions.

CHAPTER III.

THE EVOLUTION OF NATURAL SPECIES.

I. UNITY AND DIVERSITY.

The great problems of biology are found in the unity and diversity of organisms. What is the nature and origin of the unity? What the nature and origin of the diversity? And what the relation of each of these classes of facts to the other?

1. *Darwin's Explanation of the Unity of Organic Forms has been widely adopted by naturalists as by far the most probable theory; but his theory of the causes of the diversity of these forms has not met with the same general acceptance.*

He teaches that the variation, on which natural selection acts, is, for the most part, minute and indefinite variation in any and every direction, and that the progressive accumulation of one series of variations, all tending to the production of a new species, is due to natural selection. If all the offspring of any species were allowed to live out the full measure of their days and should have an equal chance to produce descendants, there would be, according to his theory, no tendency to a change of form; for variations of every kind, having an equal chance, would neutralize the divergent tendencies of each other in the general result.

Fluctuating variability, producing individual variations, is attributed for the most part to the indefinite and indirect influence of changed conditions upon the organism, the forms of variation being chiefly determined by the nature of the organism; but the transformation of a group of associated individuals is attributed to natural selection, which is the effect of external conditions tending to give advantage to the form of individual variation that is best adapted to these conditions. He says, ''Chance variation [that is, variation unaided by natural selection] would never account for so habitual and large degree of difference as that between the species of the same genus." Not only the existence of the various species of each genus, but the precise form of each species, and the instincts guiding each, are, therefore, attributed to the determining power of conditions outside of the organism, allowing of but one line of transformation in the descendants of any one species exposed to the same conditions. In order that any other line of transformation should be followed by the descendants of the same species, he considers it necessary that they should be brought under the influence of different conditions. In other words, *divergence of character presupposes exposure to diverse external conditions;* and to account for the various forms presented by the different species of the same genus, he assumes that they must have been subjected to different forms of natural selection. This theory of evolution is in strong contrast with the theory which attributes the main factors to powers residing in the organism.

2. *Divergence through Variation Protected by Isolation, and Unity through Community of Descent.*

(1) When water flows down the side of a hill from any given point, there is usually but one path that it can take; but when an animal with the power of locomotion makes the same descent there may be many paths equally open to him, and different individuals of the same species, if making the descent, will often take different paths. The course of the water is determined by laws that allow of no deviation; the course of the animal is determined by laws that allow of considerable diversity in their results; nevertheless, it is in a measure determined, and the laws that determine it are found in the relation of the powers of the animal to the natural conditions of the different paths. Paths leading down a precipitous descent may be the shortest and best for the snail, but impassable for the horse; still both the horse and the snail may find many paths that are available, and perhaps several that are equally available. The rash horses that attempt the precipitous paths break their necks, while the cautious horses that take the many safe paths are unharmed. But, shall we therefore say that the path taken by each horse making a safe descent is wholly determined by external conditions? If precipices prevent descent by every path but one, there is no opportunity for varying the course, and we regard it as being determined by the external conditions; but when the way is open in many directions, we would say that the one horse being thirsty took the path that leads to the spring, another being hungry chose the shortest road to the clover field, thus attributing the course of the animal to conditions found in the animal.

This well illustrates what I believe is true concerning the divergence of character that results in different specific forms. *I believe 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 a species distributed in isolated groups over a considerable area these varieties continue to diverge both in form and in habits till separate species are fully established, though the external conditions are the same* throughout the whole area occupied by the diverging forms.

(2) Uniformity, on the other hand, is the result of community of descent, and varies directly as the diffusion of consanguinity, or the amount of evenly distributed intercrossing. Isolation and intergeneration are opposing factors, the one tending to divergence of character, the other to uniformity; but the influence of natural selection may be in either direction, according as its action is diverse in different parts of the area or uniform throughout the whole area. When animal immigrants enter a new region in which not only the climate but the flora and fauna differ widely from those found in the home of the species, the probability is that they will succumb without leaving descendants or that their descendants will diminish with each generation till they disappear; but if the struggle is not too severe, the species will survive, and, if isolated, the divergence of character may be greatly accelerated by the effects of natural selection; for the forms that will be best fitted to succeed in life and to propagate their kind will differ in the two regions according to the conditions under which they have to compete; and the intermediate forms that are less fitted will be weeded out, and their influence in crossing with the diverging kinds that survive will be removed. It will be seen that natural selection acts as a divergent, not by its own inherent power, but by removing the intermediate varieties and thereby preventing their influence in crossing; but if the competition is severe and uniform throughout the area occupied by any species, its influence will be to lessen divergence.

That this double relation of natural selection to divergence on one side, and to uniformity on the other, was partially apprehended by Darwin, appears from his brief paragraph on Polymorphic Genera, and his fuller statements concerning the extinction of intermediate forms by means of natural selection; but the quotation given near the beginning of this chapter shows that he did not reach the conclusion which lay but one step beyond, and to which his facts so clearly point. He observed that polymorphic genera are probably most variable in the characters that are neither useful nor injurious to the species, and are, therefore, free from the influence of natural selection; and again, in another place, he observes that large genera are usually variable, that is, polymorphic, and that these same genera are the ones in which the production of new species is most rapidly progressing; but he has nowhere drawn the conclusion that freedom from rigid natural selection can in any way favor the production of new varieties and species. On the contrary, he teaches that it is only through the agency of diversity in natural selection that individual variations can be accumulated in diverging lines that become more and more distinct. (See Origin of Species, Chapter IV.)

3. *Facts in the Distribution of Hawaiian Snails.*

It was through the study of island fauna that I was first led to doubt the correctness of Darwin's theory at this point. The terrestrial mollusks of the West Indies present important differences as we pass from island to island, but it was in the Hawaiian Islands that I found the greatest difference in the species inhabiting the forests in different parts of the same island. The remarkable features in the distribution and affinities of these forms will be most easily presented by giving a brief statement of some of the facts relating to those found on the island of Oahu. This island, about 45 miles in length and 20 miles in width, is inhabited by over 200 species of land snails, represented by 800 or 1,000 varieties; and these are nearly all confined to the forests covering two ranges of mountains, the one 15 or 20 miles and the other 35 miles in length. But the most remarkable fact is not the great number of species and varieties inhabiting this small area, nor yet that all of them (with, perhaps, one or two exceptions) are peculiar to this island; but that each of these forms is confined to only a small section of this small area. Not only are the species on each of the ranges of mountains different, but those found on one range and inhabiting one continuous region of forest are not distributed at random over that region. On the contrary, each valley not more than half a mile in width and perhaps two miles in length has its own peculiar varieties, and in some cases its own species, which are found nowhere else.

As the explorer passes from valley to valley he will find six or seven quite distinct groups of forms, each group being a genus or a subgenus of the one family of Achatinellidæ. Taking any one genus and tracing its distribution from valley to valley, he will find that, as far as it extends, it is represented in each valley by one or more closely allied species, each species being represented by several varieties. One species may be confined to a single valley, or it may extend over several, being represented in each by varieties peculiar to that valley. The more widely divergent forms of one group or genus will be found in the valleys that are most distant from each other. That is, if the genus is present in all the valleys, the most divergent forms will be found at the opposite ends of the mountain range, while intermediate forms will be found in the intermediate valleys. Allied species occupying neighboring localities pass into each other by many gradations of form and color, while those that are separated by a distance of 8 or 10 miles or more can not be connected by minute gradations without bringing in some of the forms found in the intermediate territory.

Such are the main facts concerning these forms when viewed in their relation to each other. Let us now consider the external conditions. Does the theory that all divergence of character is due to exposure to diverse conditions find confirmation, or the opposite, in the facts connected with these Hawaiian snails?

4. *Diversity of Natural Selection not a Sufficient Explanation of the Diversity of Species.*

Natural selection depends upon external conditions which are either favorable or unfavorable to the success and propagation of the organisms under consideration; and difference in natural selection must depend upon difference in the nature of the external conditions that affect survival. Now, returning to the case of the nearly allied arboreal species in the valleys near Honolulu, can we find any diversity affecting survival in the conditions to which they are exposed? In many cases we find them occupying the same species of trees, and, accordingly, if their habits of feeding are different, we must attribute this difference to spontaneous variation rather than to the influence of external conditions. Extending our observations to the climate and soil, we find the conditions unvaried, we might well say, identical; for the geological foundation of the whole mountain range is volcanic basalt without the least limestone, and the soil in these rugged valleys is not varied by the presence even of volcanic ash, while the conditions of heat and moisture are the same on the same side of the mountain crest. The vegetation in each valley is essentially the same, and distributed in a similar way; for certain shrubs and trees occupy the lower grounds and others the steep slopes and ridges that rise above. If the species of mollusks which we are studying have any enemies they are found in the forest regions throughout the island. No insect or reptile, no bird or mammal, found on the island is limited to a district of only 2 or 3 miles extent.

As we fail to find any cause for the divergences of character in the external conditions, we must believe either that the conditions are more diversified than they appear to be, or that the causes of change in these cases belong wholly to the nature of the organism. That the former supposition is not the true one seems to me to be sufficiently proved by the following facts and considerations:

(1) If the divergence of character was due to difference of natural selection resulting from difference in external conditions, we should expect that the distribution of species would bear some marked relation to the amount of rainfall, which, owing to the northeast trade winds, is considerably greater on the northeast side of the mountain range than on the southwest side. On the contrary, we find that species of the same group, found in valleys on the same side of the range, but 30 or 35 miles apart, are far more divergent from each other than are those found on opposite sides of the range but at points much nearer. Assuming that they have migrated from a common center, the distance between two species measures in a rough way the relative number of generations that have passed since their ancestors parted company, and the degree of divergence is in proportion to the time and degree of separation rather than in proportion to the degree of difference in external conditions.

(2) This law of distribution is found, not simply in the case of a few related forms, in which it might be supposed that the diversity of conditions was real, though not apparent, but is the general law according to which the 200 species and 800 or 1,000 varieties of Achatinellidæ found on this island are for the most part distributed. This law also controls the distribution of mollusks on the neighboring islands and in many parts of the world.

(3) If we assume that the divergence is due to the diversity of natural selection, we must hypothecate a series of conditions affecting survival presenting increasing differences with each additional mile.*

5. *The Causes of the Divergence must lie in the Independent Action of the Segregated Sections of the Original Stock.*

For my part I find it easier to believe that the causes of divergence of character in these forms that are, so far as we can discover, exposed to the same conditions, exist in the organism.

(1) We know that the individual variations in specimens of one species found on one tree are often very considerable.

(2) Unless the degree and kind of variation is *invariable* in separated groups of the same species, it is self-evident that there must be a tendency to divergence of character.

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* See Plate II, figs. 11–25.

(3) So far as statistical observation has been directed to this subject, I believe it has been found that complete correspondence of averages is found in the measurements of mankind only when the groups compared are sections of one homogeneous community thoroughly related by community of descent. There is, therefore, reason to believe that the laws of heredity check divergence and secure uniformity in proportion to free intermarriage and community of descent, and that, if complete separation exists for many generations between two groups of the same race, divergence will take place though the external conditions are the same.

We therefore arrive at the conclusion that, while variation and isolation are the essential factors in diversity of evolution, and intercrossing and unity of descent the essential agents in uniformity of evolution, natural selection may be an important ally on either side.

II. Selection as an Explanation of Evolution.

In discussing this subject we shall consider, 1, What selection in its different forms does not explain; and 2, How far selection is determined by external nature.

1. *What Selection does not Explain.*

(1) *It can not account for the introduction of coöperative and anticipatory action.*

Evidently it can not account for the powers on which it depends for its action. Now, natural selection presupposes the general power possessed by every organism, of coöperative and anticipatory action, based upon a discrimination between the probable results of different actions, and directed toward the maintenance of that ideal state in the actor which we call life.

While still in the egg or attached to the parent, anticipating the need of organs adapted to a new environment, the organism builds in different ways the most wonderful structures, all of which are transformations of its own simple colorless fluid. This we call growth and development.

Having entered on independent life, it anticipates the tendency of work and waste to produce exhaustion, and forefends this result by appropriating portions of dead, extraneous fluid matter, transmuting it into its own living fluids, from which it rebuilds the wasting structures. This is assimilation.

Anticipating its need of special substances to supply this continual consumption, it executes many movements in order to reach advantageous substances and to avoid injurious ones. This is accommodation.

Anticipating the inevitable death that approaches, it produces young of its own kind, which shall perpetuate the race. This is reproduction.

Anticipating the fact that external nature is subject to change, and that, even under unchanged conditions, better adaptations are often possible, it sends forth its offspring endowed with various powers, as experiments in different directions, thus increasing the probability that some will survive. And this is called variation.*

Being thus wonderfully endowed, having been placed in a world in which some of the resources were fully adapted to sustain them, while other resources were only proximately available, and where many of the conditions were undergoing gradual change—such beings, in such a world, would be constantly pressing into new spheres of existence and adapting themselves to the changing world; for from the very nature of their powers there would be a greater propagation of those better adapted and an inferior propagation of those less adapted to the various conditions into which their segregating powers had driven them. Now, this propagation, according to adaptation, this survival of the fittest, this selection, is the interaction of these powers with external nature, and, therefore, can not account for the existence of the powers, though their perfection may be due to their continuous action.

(2) *Selection can not explain the division of one race into several races.*

Again, we see what selection can not explain by considering the nature of the process. The survival of the fittest results in the breeding together 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*

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* The importance of *anticipatory action* is emphasized by Benjamin Kidd in "The Principles of Western Civilization." His term is "projected efficiency." The same power is discussed by Prof. James Ward, of Edinburgh, under the term "subjective (or hedonic) selection, * * * a teleological factor * * * found to belong to all things living." (See Naturalism and Agnosticism, Vol. I, p. 294, and Vol. II, pp. 92, 161.) "Accommodation," as used by Prof. J. Mark Baldwin, covers all acquired adjustments of the individual to the environment. (See his Development and Evolution.) Functional variation is used by Hertwig in the same meaning. "Acclimatization" as used by Prof. Charles B. Davenport covers all forms of accommodation to unfavorable conditions. (See Experimental Morphology.)

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.

(3) *Selection does not explain the establishing of unnecessary characters.*

Again, selection can not explain the divergent transformation of forms distinguished from each other in qualities that are not related to their success in gaining a living and propagating their kind. As illustrations of such transformation may be mentioned beautiful arrangements of color that can not be attributed either to natural selection or to sexual selection; for example, the patterns with which many Hawaiian snails are ornamented, which can not be of use either in attracting mates or in gaining a living.

2. *Selection—How far Determined by External Nature.*

Passing to the next point, we inquire whether change in the character of the selection affecting any organism is wholly determined by change in external nature? Or can change in the character of the selection be initiated and maintained through change in the organism, without any change in the environment?

(1) *Herbert Spencer's view.*—Spencer distinctly affirms that the latter method of change is impossible. The following are his words: "That there may be continuous changes in organism, there must be continuous changes in incident forces." And, again, "At first, changes in the amounts and combinations of external inorganic forces, astronomic, geologic, and meteorologic, were the only causes of the successive changes undergone by organisms. [In time, however,] the actions of organisms on one another became new sources of organic modifications." (Principles of Biology, secs. 169, 170.)

Spencer rests his denial of the freedom of the human will on the assumption that all vital activities are predetermined by activities in the environment.* It is evident that if our natural powers and our present conditions are so determined by the environment that we can produce but one set of actions, then no effort on our part, either individual or collective, can in the least affect the result; for we can not change our circumstances without acting, and our actions are already determined by our circumstances.

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* See Principles of Psychology, sec. 220.

(2) *External nature furnishes the means and occasions, but not the cause.*

But to return to our question, can anything be surer than that through the activities of the organism changes in its relation to the environment are often produced; and that through these changes the character of its success is changed, and so the character of its selection.* As we have already observed, it is by virtue of its power to strive for the continuation of its life that an organism is an organism; and selection is the direct result of varying degrees of survival in the exercise of this power. We see, therefore, that the doctrine, common among a certain class of evolutionists, that the environment makes the organism, rests on a false assumption, the introduction and perpetuation of which has been favored by the ambiguities covered by the phrases in use. *External nature can never furnish more than the means, occasions, or opportunities for vital phenomena.* The power to use these means in maintaining life lies wholly with the organism, and the degrees of success which it achieves are produced by this power, and not by the environment. So far as the environment consists of organisms, each species of this organic environment is working for its own survival, and not for the survival of any other species to which it stands in the relation of environment. The bees take honey from the flowers for the preservation of themselves and their kindred; and the flowers make the bees distribute their pollen, thus securing more vigorous seed than could be gained by self-fertilization; each species working for its own preservation and perpetuation.

Another cause of confusion has been the habit of speaking of the transforming power of selection as if it were a special power, or form of power quite distinct from the power of variation; whereas, it is only one of the laws expressing the relations that exist between the different results of organic activity. Selection is the superior propagation of adapted forms, through the dependence of the degrees of propagation on the degrees of adaptation produced by variation. Every variation of the organism may be regarded as more or less adapted, and the survival of each, according to its degree of adaptation to the natural environment surrounding the group, is natural selection; but this diversity of survival is the direct result of the varying adaptation of the organism. The transforming power of natural selection is, therefore, not a different *power* from variation, but it is rather a direct *result* of variation.

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* See the description of active or endonomic selection given in Appendix II, and of other forms of autonomic selection in Chapters V–VIII.

(3) *Change of selection without change in the environment.*

Darwin's language in describing the relation of these different factors has been shaped by the relation in which man stands to the animals he selects for breeding. Here we speak of the selecting power as being in the man who determines what animals shall survive and breed, and the power of variation as being in the organism which furnished the varieties for his selection. But in nature there is no power standing outside of the organism and determining what kinds shall propagate. Any kind, and every kind, that can hit on any means of support will survive and have the opportunity to propagate. The means and methods of survival are often very various, and nature shows no preference for one method above another. It is only through the different degrees of survival that there comes to be any selection, and these degrees of survival depend on the different powers presented by the different varieties of the organism.

If we wish to draw a true parallel between natural selection and rational selection, we must consider both wild and domestic creatures as gaining opportunity for propagation by adapting themselves to the environment; the one class varying so as to be the best able to perpetuate its kind in the struggle for life among irrational creatures, and the other class by varying so as to be the most pleasing to man, and through his care and protection gaining a chance to live and propagate. The one class adapt themselves to the natural environment, the other class to the rational environment. From this point of view we see that in both classes propagation depends on adaptation, and that adaptation depends on variation; and this dependence is selection. *We must, therefore, conclude that change in the character of the selection may be initiated and continued through change in the organism without any change in the environment, except what is produced by the action of the organism.*

(4) *Diversity of selection due to power of varied adaptation.*

In more general terms, the relations of the organism to the environment are determined by the power of the organism to use the environment; this power of use being defined as the power of varied and discriminative action with reference to the maintenance of life through the subordination of present means to future ends. This power is found in every living organism, but never in the inorganic world. We can not conceive of a living organism entirely destitute of the power of adaptive and discriminative action; for this is the fundamental distinction between the living and the nonliving. Nor can we conceive of the prolonged existence, in such a world as this, of any organism entirely destitute of the power of variation, for every individual of such a species would be exactly like every other; and there could be no progressive adaptation of its powers to the changing environment, through natural selection or any other process.

(5) *Must distinguish between the cause and the conditions of evolution.*

In view of these several conditions, we may safely attribute selection and the other laws of evolution resulting from adaptive action to the organism as their cause, though we know that the environment furnishes the sum of the conditions, under some combination of which the cause must act.

(6) *Statistical proof of natural selection.*

H. M. Vernon, in his Variation in Animals and Plants, 1903, pp. 341–345, gives statistical proof, quoted from Dr. Bumpus,* that the English sparrow in the Northern States of America, when suffering from heavy storms of rain, snow, and sleet, loses by death more of those presenting certain characters than of others. The conclusion which Bumpus draws is that "Natural selection is most destructive of those birds which have departed from the ideal type, and its activity raises the general standard of excellence by favoring those birds which approach the structural ideal." Vernon shows from the figures given by Bumpus that though the longest and shortest birds are most exposed to death from such a storm, the average length of the birds that recovered from the effects of the storm after being captured was 1.27 per cent less than that of the birds that perished. The average weight of those that recovered was 2.38 per cent. less than that of those that perished. If these averages represent blastogenic (or inherited) characters it would seem that the species is undergoing transformation through exposure to a climate to which it is not yet fully adjusted.

III. DISCONTINUITY OF SPECIES.

In his volume entitled "Material for the Study of Variation," published in 1884, Bateson points to the lack of correspondence between the diversity of physical environments and the diversity of specific forms as a feature unexplained by the theories of either Lamarck or Darwin. On page 5 of his book we read:

> According to both theories [the Lamarckian and the Darwinian] specific diversity of form is consequent upon diversity of environment, and diversity of environment is thus the ultimate measure of diversity of specific form. Here, then, we meet the difficulty that diverse environments often shade into each other insensibly and form a continuous series, whereas the specific forms of life which are

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* See Biol. Lectures, Wood's Hole, 1898, p. 211.

> subject to them on the whole form a discontinuous series. * * * Temperature, altitude, depth of water, salinity, in fact most of the elements which make up the physical environment are continuous in their gradations, while as a rule the forms of life are discontinuous. Besides this, forms which are apparently identical live under conditions which are apparently very different, while species, which though closely allied are constantly distinct, are found under conditions which are apparently the same.

He suggests that the explanation of this lack of correspondence must be sought in the organic group, and not in its environment; and that in the study of variation is the chief hope though even that may fail (p. 17).

I entirely agree with Mr. Bateson in regard to the importance of variation and of the factors in the species that control variation; and prominent among these factors I find either the power of free communication and intergeneration or the lack of this power. When a species possessing very limited powers for migrating and very rare opportunities for transportation is surrounded by a mass of species having the usual powers and opportunities, the natural result is that many colonies from the species having very limited powers become completely isolated from each other and from the original stock, while the surrounding species of plants and animals are not isolated from the groups of the same species in other places. A further result is that the isolated colonies become divergent, while the species having powers that prevent isolation remain the same as in the original home. The isolated groups being prevented from crossing with each other, there is nothing to prevent each group from establishing its own special methods of dealing with the environment, and thus subjecting itself to special forms of selection, though dealing with the same environment. No better examples can be found of the divergence of isolated groups while exposed to the same environment than those presented by the arboreal snails of the Hawaiian Islands and of some other regions.

The probabilities are completely reversed in the case of a species possessing unusual powers for migrating, or extraordinary opportunities for transportation. For it often happens that groups of such a species, occupying districts very unlike, not only in climate but in the prevalent species of plants and animals, will maintain free communication and intergeneration with each other, and thus be kept to essentially one type. Good examples of unity of type maintained notwithstanding long exposure to diverse conditions are found in the case of certain species of birds and insects possessing great powers of flight.

The principle underlying both classes of cases is that free intergeneration insures unity of type, and that the prevention of free communication and of free crossing prevents the operation of reflexive selection* between the isolated groups, and also opens the way for diversity in the use of the environment, and so leads to diversity in other forms of selection. Isolation, therefore, coöperating with the power of variation and with the principle of selection of other forms than natural selection, goes far toward explaining the phenomena which we have been considering, and which are essentially the same as those which Mr. Bateson has cited as being in pressing need of explanation. Discontinuous variation explains the lack of intermediate forms in certain cases, but it is not the necessary explanation in every case.

The related subject of mutation is briefly considered in Chapter V, at the end of section III. Those interested in the subject of the discontinuity of closely related species will find an interesting summary of the facts and interpretations in "The Method of Evolution," by Professor Conn, pages 35, 115 to 139, 359.

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* Reflexive selection is described in Appendix II, I, 8, (3), as "depending on the relations of the members of a species to each other." The most familiar forms of reflexive selection are sexual and social selection. It is, of course, manifest to every one that two completely separated groups of the same species can have no influence over each other through sexual and social selection. Other forms of reflexive selection are considered in Chapter VI; also the fact that there are endonomic forms of environal selection.

CHAPTER IV.

DIVERGENCE UNDER THE SAME ENVIRONMENT.

EXPLANATION OF PLATE I.

Plate I presents 21 species of 8 genera of one family found on five of the islands of the Hawaiian group. These islands are within sight of each other, having the same climate and much the same vegetation, and (with the exception of the different forms of snails) the same species of animal life; and yet how great the diversity presented by the species of the same genus, not to mention the greater divergence attained by the different genera. These eight genera, and the two genera represented in Plates II and III, all belong to the family of Achatinellidæ, found in no part of the world outside of the Hawaiian Islands. These genera, though differing widely in form and habits, have one shell-characteristic which does not occur in the same degree in snail shells found in other parts of the world. It will be observed that the small glassy genus Leptachatina (fig. 5), and the minute Auriculella, with a sharp plate in the aperture (fig. 3), are like the much larger shells of the other genera, in that they have a twist in the columella. The character appears in a greater or less degree in all the ten genera by which the Achatinellidæ are represented.

Of these eight genera, Carelia is found only on Kauai, Apex and Bulimella only on Oahu, while Amastra (and probably Leplachatina), is found on all the islands of the group, and Auriculella, Laminella, and Partulina are found on the central islands, that is, on Oahu, Molokai, Landi, and Maui. The one arboreal species I have received from the island of Hawaii is either a Partulina or a Newcombia, the specific name being *physa* (Newcomb). The typical forms of Newcombia are found on Maui and Molokai. Laminella and Partulina find special development on Maui, Molokai, and Lanai, where they are represented by many species. The genera most characteristic of the island of Oahu are Bulimella, Achatinella, and Apex. The most nearly allied species from different islands do not completely intergrade as do those from the same island. For example, *Partulina splendida* of Maui (fig. 14) does not completely intergrade with *P. virigulata* of Molokai (fig. 12), or with *P. variabilis* of Lanai (fig. 13), as it does with certain other species of *Partulina* found on Maui. The species of this genus have been so chosen as to present from each island the form most nearly related to *Partulina splendida*. So also in the case of the Laminella, it is not the most divergent species that have been chosen, but the most closely related of those found on the different islands.

In the case of arboreal species, the isolation between those inhabiting the forests of East Maui and those inhabiting the forest of West Maui is almost as complete as if they inhabited separate islands; for the open grass land separating the two masses of forest-covered mountains is as complete a barrier against direct migration as would be a salt-water channel. There is, however, a somewhat better chance of transportation by human agency across grass land than across an equal width of water.

Carelia is always dextral in form; and I think it is terrestrial in its habits. Amastra and Leptachatina, which are almost always found on the ground, are with extremely rare exceptions dextral in form; while of the arboreal genera, Newcombia and Laminella are almost always sinistral, and Auriculella, Apex, and Partulina have some species constantly sinistral, others constantly dextral, and others that assume either form. Achatinella and Bulimella (represented in Plates II and III), are constantly arboreal in habits, and both dextral and sinistral in the forms assumed.

The following abbreviations are used in the "Notes" on the species given in Plates I, II, and III.

Fer. = Ferussac; Gk. = Gulick; Migh. = Mighels; Nwc. = Newcomb; Pfr. = Pfeiffer; Rv. = Reeve; Sm. = Smith; Swn. = Swainson; D = dextral in form; S = sinistral in form; $D > S$ = the majority are dextral; $S > D$ = the majority are sinistral; $S - D\frac{1}{500}$ = sinistral with the exception of about 1 in 500.

NOTES ON THE SPECIES.

FIG. 1. *Carelia cocklea* (Rv.) D. From the island of Kauai. Examination of the organs will probably place it with the Achatinellidæ.

FIG. 2. *Amastra nucleola* (Gould) D. From Waiole, Kauai.

FIG. 3. *Auriculella auricula* (Fer.) $D > S$. This species, like others of this genus, is found on the leaves of trees and shrubs. Its habitat is the eastern portion of the forest region of the island of Oahu This specimen is from the valley of Palolo.

FIG. 4. *Apex apicatus* (Nwc.) $D > S$. From Wahiawa, Oahu. Also found in Helemano and Ahonui.

FIG. 5. *Leptachatina fumosa* (Nwc.) D. Found on the ground under dead leaves, in damp forest regions from Nuuanu to Palolo, on the island of Oahu. This specimen is from Palolo.

FIG. 6. *Laminella sanguinea* (Nwc.) S. Found in Helemano and Wahiawa and the intervening regions on the island of Oahu. This specimen is from Helemano.

FIG. 7. *Laminella citrina* (Migh.) S. From the island of Molokai.

FIG. 8. *Laminella tetrao* (Nwc.) S. From the island of Lanai.

FIG. 9. *Laminella venusta* (Migh.) S. From Lahaina, West Maui.

FIG. 10. *Laminella bulbosa* (Gk.) S. From Kula, East Maui.

FIG. 11. *Partulina dubia* (Nwc.) D. This is a rare species distributed over a number of valleys of the island of Oahu from Waianae to Kalihi. This specimen

is probably from Kalihi. No other species from the Hawaiian Islands seems to so closely resemble the Partula found on many of the islands of the Pacific. Still it must belong to the Achatinellidæ, for it completely intergrades with *Partulina densilineata*, which presents the peculiar twist of the columella, the most constant shell-character of the Hawaiian family of snails.*

FIG. 12. *Partulina virigulata* (Nwc.) D > S. From the island of Molokai.

FIG. 13. *Partulina variabilis* (Nwc.) S. From the island of Lanai.

FIG. 14. *Partulina splendida* (Nwc.) D > S. From Lahaina, West Maui.

FIG. 15. *Partulina plumbea* (Gk.) D. From Kula, East Maui; found on the trunks of trees several thousand feet above the sea level.

FIG. 16. *Newcombia cumingii* (Nwc.) S. From Makawao, East Maui.

FIG. 17. *Amastra turritella* (Fer.) D. Found on dead trees from Waiawa eastward to Keawaawa, island of Oahu. This specimen is from Palolo.

FIG. 18. *Amastra violacea* (Nwc.) D. From the island of Molokai.

FIG. 19. *Amastra magna* (Adams) D. From the island of Lanai.

FIG. 20. *Amastra mastersi* (Nwc.) D. From Lahina, West Maui.

FIG. 21. *Amastra nigra* (Nwc.) D. From Kula, East Maui.

The Darwinian theory explains the unity of form in the different genera and species of one family by the theory that they are all descended from one original intergenerating stock. The diversity in the forms is explained as the result of variation, with diversity in the *forms of selection produced by exposure to different environments*. In explaining the divergence in the genera of this family, I think, we shall come nearer to the facts if we attribute the diversity in the selection, to which they have been exposed for countless generations, to *diversity in the methods of using the environment adopted by completely isolated groups*. The *divergence* in many of the closely related species, found on the same species of trees in successive valleys on the same mountain range, is, I think, *due to isolation and variation, without any difference in the forms of selection.*

EXPLANATION OF PLATE II.

This plate presents 25 species of Achatinella, a genus of arboreal snails found on the island of Oahu, and most of them confined to districts from 1 to 3 or 4 miles in extent. Achatinella is one of ten genera of the Achatinellidæ, of which there are between 200 and 300 species and over a thousand varieties, on this island only 40 miles long. Eight of these genera are given on Plate I, and one on Plate III. This plate illustrates the relationship of species distributed in different valleys on the same island. The letter attached to each figure designates the valley or small district in which the specimen figured was found. The position of this valley or district on the island is easily

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* A careful comparison of the internal structure of this species with the structure of the Partula of the South Pacific might perhaps reveal points of special interest in the relations of the two groups.

discovered by reference to the map of Oahu preceding Plate II, where the same letters are used to designate positions. It will be observed that underscored letters are used to designate positions on the northeast side of the main mountain range, and that Roman letters are used to designate the positions on the southwest side of the same range. These are so arranged that the valleys indicated by the two forms of any one letter are nearly opposite to each other.

The twenty-five species presented in this plate would have to be considered as one species if we accepted the statement that the finding of completely intergrading forms between two types proves that they are varieties of the same species. If, on the other hand, we adopt the statistical method of testing species,* these, and many more found in the forests of the same mountain range, will have to be classed as species. The collection of the species and varieties of this genus, made by me from 1850 to 1852, present a complete series of intergradations between the larger forms found on the trunks of the candle-nut tree in the eastern valleys of Oahu, and the small forms found on the leaves of the lobelia and other shrubs in the western valleys of the island, where groves of the candle-nut tree abound, occupied more or less by species of Bulimella, but neglected by the representatives of the genus Achatinella. As no one will maintain that these most divergent types of the genus belong to the same species, the existence of such a series of intergrading links becomes a strong argument for the belief that divergent forms properly ranking as species have arisen from one original species, through the cumulative effects of variation coöperating with a series of isolations, each isolation lasting for many generations before the next occurs.

The genera most characteristic of Oahu are Achatinella, Bulimella, and Apex; for, with the exception of two or three species of Achatinella found on the island of Molokai, they are limited in their distribution to this island. Their distribution in the different districts of the island is probably due to the adaptation of Bulimella to a damp climate, and of Achatinella to a region of dense shade, but of less rain, and of Apex to a comparatively dry climate. As regards rainfall, the northeast side of the main range catches the trade winds as they come from the ocean, and receives the heaviest fall; on the southwest side of the same range there is less rain; and on the shorter range, on the southwest side of the island, there is still less rain. In the first region we find Bulimella and a very few Achatinella; in the second region

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* The explanation of Plate III brings out the fact that the individuals representing intermediate forms are very rare compared with those of typical forms. Such species meet the statistical test.

both Bulimella and Achatinella in the shady valleys, with Apex on the comparatively sunny ridges; and in the third, several abundant species of Apex, and but one species of Bulimella, and but one of Achatinella, both of these being extremely rare.

NOTES ON THE SPECIES.

FIG. 1. *Achatinella zonata* (Gk.) S. From Pupukea.
FIG. 2. *Achatinella albescens* (Gk.) S. From Pupukea.
FIG. 3. *Achatinella recta* (Nwc.) S. From Kawailoa.
FIG. 4. *Achatinella herbacea* (Gk.) S. From Kawailoa.
FIG. 5. *Achatinella delta* (Gk.) S. From Wahiawa.
FIG. 6. *Achatinella rhodorhaphe* (Sm.) S. From Wahiawa.
FIG. 7. *Achatinella pygmæa* (Sm.) S. From Ewa.
FIG. 8. *Achatinella ligata* (Sm.) D. From Ewa.
FIG. 9. *Achatinella analoga* (Gk.) S. From Halawa.
FIG. 10. *Achatinella colorata* (Rv.) S. From Halawa.
FIG. 11. *Achatinella adusta* (Rv.) S. From Pauoa.
FIG. 12. *Achatinella castanea* (Rv.) S. From Pauoa.
FIG. 13. *Achatinella olivacea* (Rv.) S. From Pauoa.
FIG. 14. *Achatinella dunkeri* (Cuming) S. From Makiki.
FIG. 15. *Achatinella producta* (Rv.) D > S. From Makiki.
FIG. 16. *Achatinella buddii* (Nwc.) S. From Makiki.
FIG. 17. *Achatinella johnsonii* (Nwc.) S > D. From Manoa.
FIG. 18. *Achatinella stewartii* (Green) D > S. From Manoa.
FIG. 19. *Achatinella fuscozona* (Sm.) S. From Manoa.
FIG. 20. *Achatinella trilineata* (Gk.) S. From Palolo.
FIG. 21. *Achatinella varia* (Gk.) S — D $\frac{1}{500}$. From Palolo.
FIG. 22. *Achatinella bacca* (Rv.) D. From Palolo.
FIG. 23. *Achatinella plumata* (Gk.) S. From Waialae.
FIG. 24. *Achatinella diversa* (Gk.) S. From Waialae.
FIG. 25. *Achatinella abbreviata* (Rv.) D. From Waialae.

EXPLANATION OF PLATE III.

The purpose of this plate is to illustrate the variations and intergrading forms of closely related species of the Achatinellidæ. The 25 shells figured in this plate are found in the northwestern portion of the island of Oahu, and are regarded as belonging to four species, of which *Bulimella ovata* Nwc. is presented under ten variations, five being of the dextral form (see figs. 6 to 10), and five of the sinistral form (see figs. 11 to 15). Of these figure 10 is found in Hakepuu, and the rest in Kahana. Figures 1 to 5 are of *Bulimella bulimoides* Swn., found in Kawailoa; figures 16 to 20 are of *Bulimella obliqua* Gk., found in Kahana; figures 21 to 25 are of *Bulimella rosea* Swn., of which figures 21 to 24 are found in Wahiawa, and figure 25 is found in Helemano. Intergrading forms are found between figure 5 of this plate and *Bulimella glabra* Nwc.; between figure 8 of this plate and *Bulimella oömorpha* Gk.; between figure 15 of this plate and *Bulimella rotunda* Gk.

The relative numbers in which these different variations occur are roughly indicated in the following table, in which the numbers not inclosed in parentheses correspond with the figures in Plate III, while the number in parentheses below each one of these indicates approximately the relative frequency in which it was found.

1	2	3	4	5	6	7	8	9	10	11	12	13
(200)	(150)	(100)	(60)	(30)	(200)	(200)	(200)	(200)	(100)	(200)	(200)	(200)

14	15	16	17	18	19	20	21	22	23	24	25
(100)	(60)	(1)	(200)	(200)	(200)	(60)	(30)	(300)	(45)	(15)	(15)

The metropolis of *Bulimella rosea* is Wahiawa, where the most abundant type of coloring is seen in figure 22, which is snowy white with a pink lip. In Helemano district, the shells of this species are somewhat smaller, with the lip more frequently white, and the body of the shell not as snowy white as is usually the case in the metropolis. Figure 21 is a comparatively rare variety of *B. rosea*, white throughout and intergrading with *B. ovata* through a nearly white variety of the sinistral form of that species, occurring in Kahana in the proportion of perhaps one to a thousand of the normal specimens of the species. Again, in figure 16, we have a very rare form connecting *Bulimella obliqua* with *Bulimella ovata*.

OAHU THE METROPOLIS OF THE ACHATINELLIDÆ.

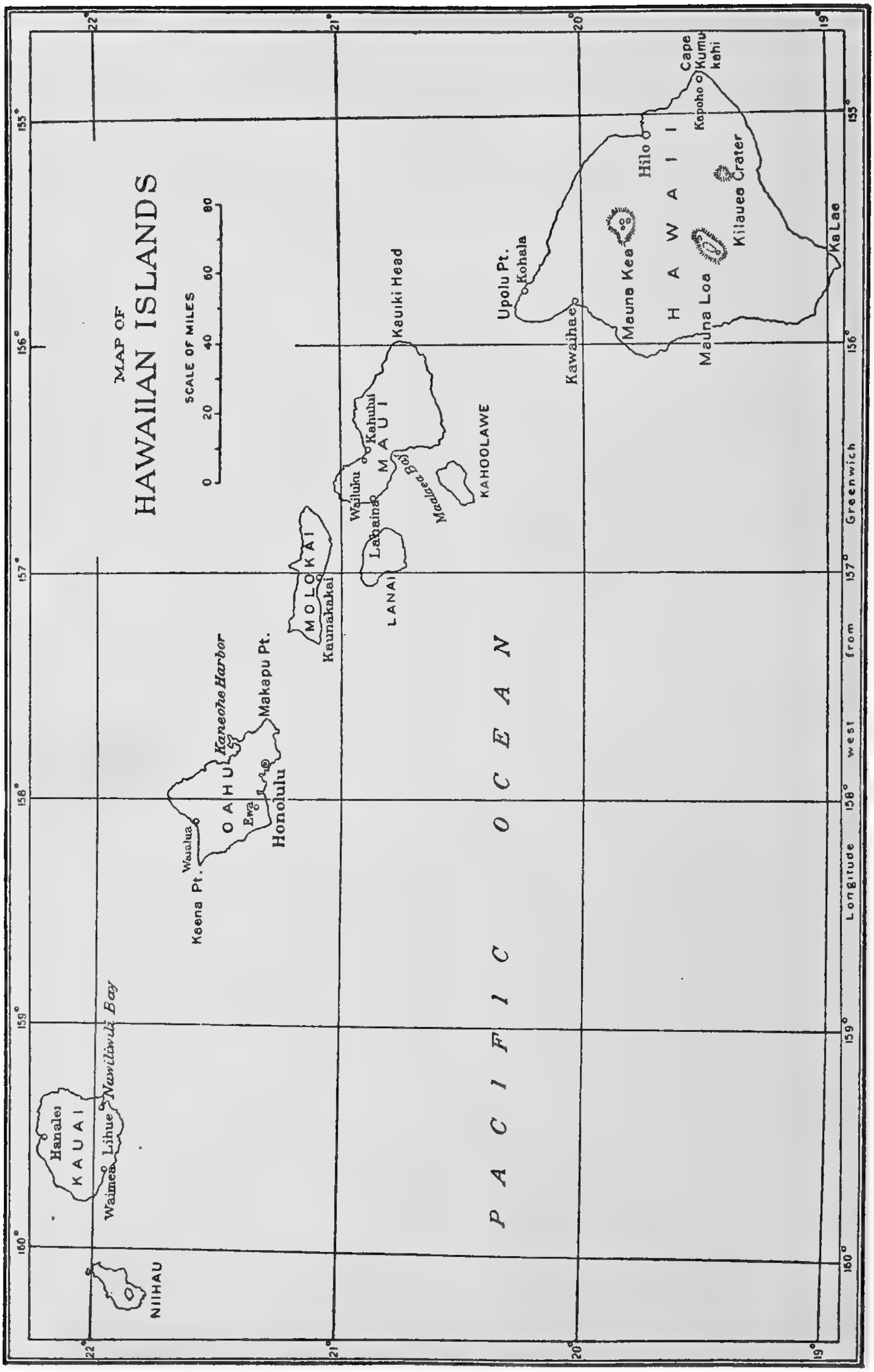
The island of Oahu may be regarded as the metropolis of the Achatinellidæ, for on this island we find 8 of the 10 genera, while on Maui and Molokai together we find 7 genera, and on Kauai 3 genera. Sufficient attention has not been given to the land snails of Hawaii to enable us to give a full report; but I am told that there is an unusual development of Succinea on that island, while the Achatinellidæ are but very meagerly represented. One explanation of the small development on the island of Hawaii of the family of snails which is so fully developed on the island of Oahu is found in volcanic eruptions, which on the island of Hawaii have from time to time destroyed the forests till recent years; while on the island of Oahu it is probably hundreds of thousands of years since such complete destruction of the necessary conditions of existence for these creatures has occurred.

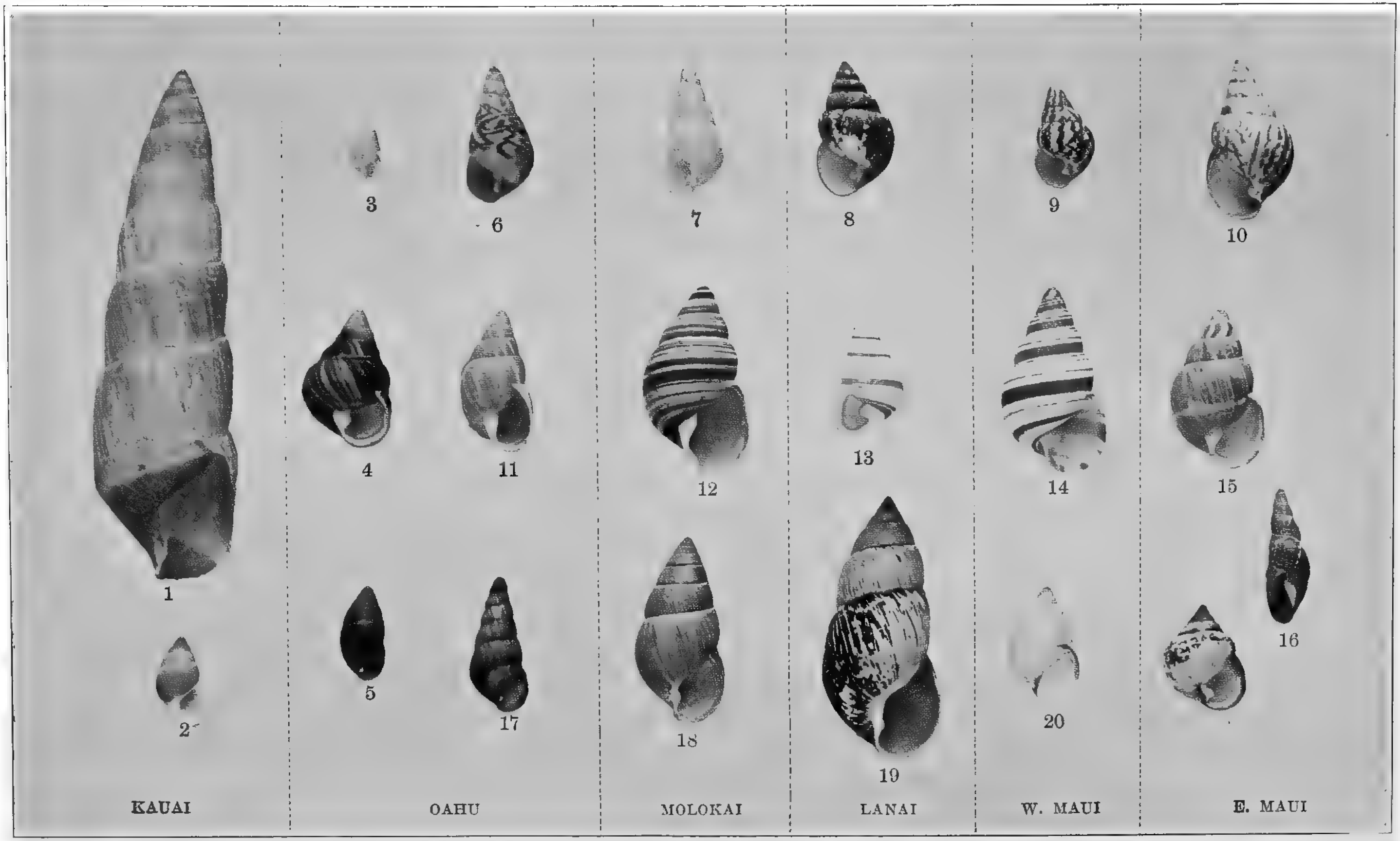
In simple and tasteful bridal array was the little Church of the Epiphany Wednesday evening, where great chrysanthemums set among the glowing tapers of the altar and banks of shining greens lent their beauty to the setting for the marriage of Miss Laurette Rockwell, daughter of State Senator T. D. Rockwell, and Mr. Lloyd G. Bowers of Birmingham, Ala. As Rev. Cameron Morrison took his place at the chancel steps, the processional from Lohengrin brought the bridegroom with his best man, Mr. Henry Perry, also of Birmingham, to the altar, who awaited the small bridal party led by Miss Helen Scoby, the maid of honor.

The radiant bride came with her father in a gown of ivory tinted taffeta, softly veiled in georgette. It was of round length, with folds of the taffeta for trimming effectively carrying out the simple design. From her shoulders fell the long train, gracefully overdraped with a long veil, plaited to a coronet of rose point lace. She carried a bouquet in shower effect, fashioned of Ophelia roses and lilies of the valley, combined with maidenhair fern.

Miss Scoby was stunning in

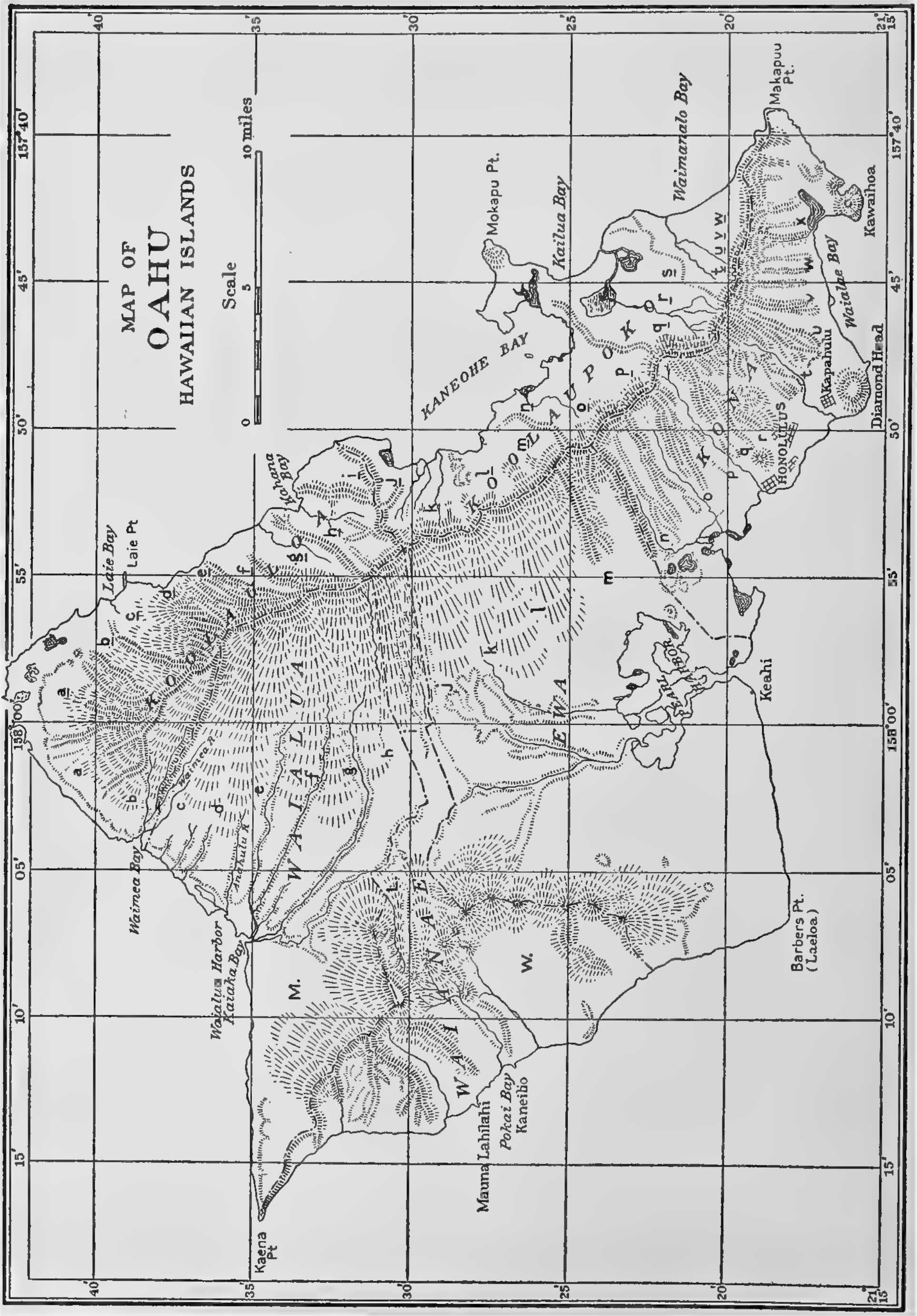
PLATE A.

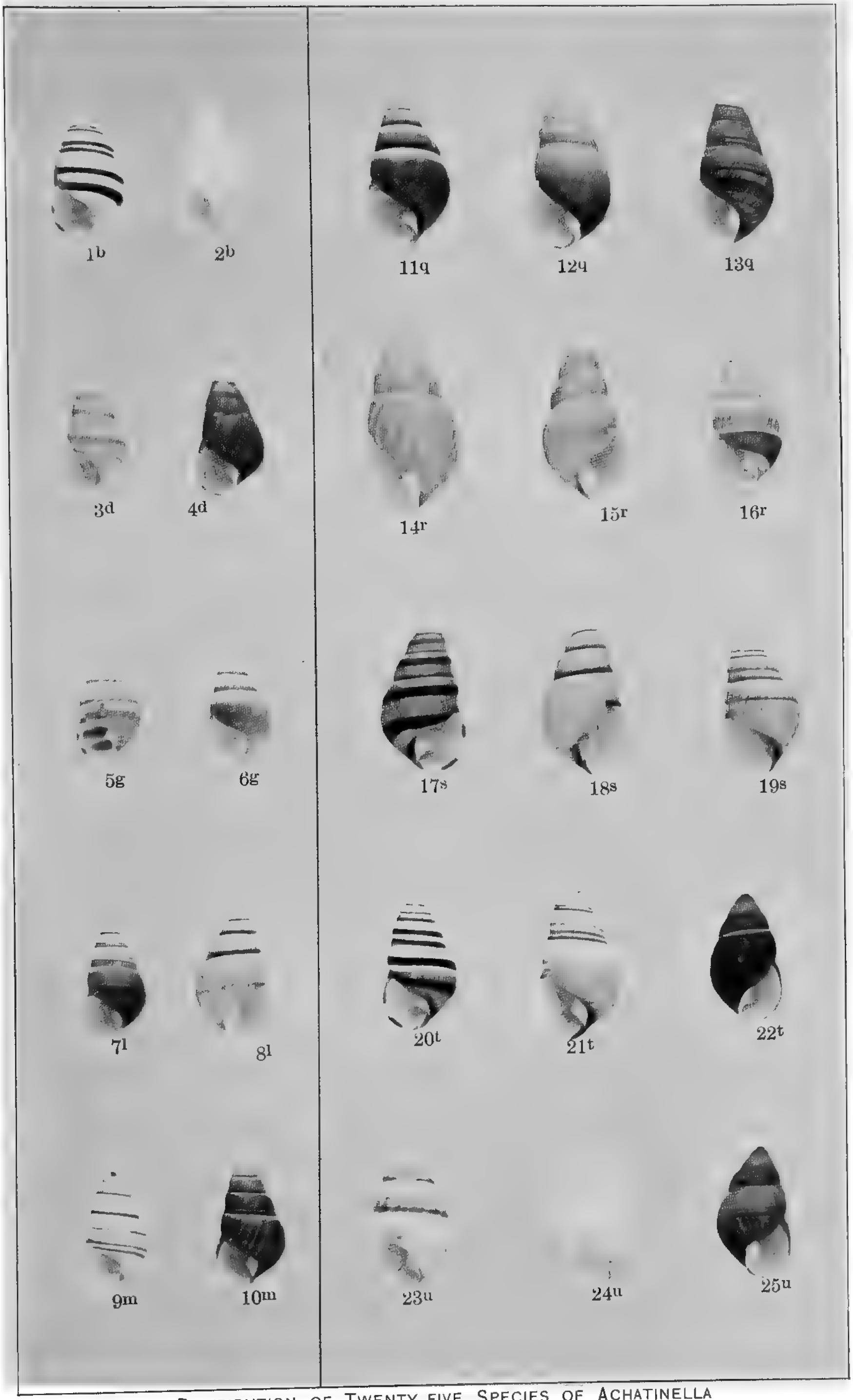

MAP OF
HAWAIIAN ISLANDS
SCALE OF MILES
0
20
40
60
80
NIIHAU
KAUAI
Hanalei
Lihue
Waimea
Nawiliwili Bay
OAHU
Waialua
Kaena Pt.
Ewa
Honolulu
Kaneohe Harbor
Makapu Pt.
MOLOKAI
Kaunakakai
LANAI
Lahaina
Wailuku
Kahului
MAUI
Maalaea Bay
Kauiki Head
KAHOOLAWE
HAWAII
Upolu Pt.
Kohala
Kawaihae
Mauna Kea
Mauna Loa
Hilo
Kilauea Crater
Kapoho
Cape Kumukahi
Ka Lae
PACIFIC OCEAN
Longitude west from Greenwich
155°
156°
157°
158°
159°
160°
19°
20°
21°
22°



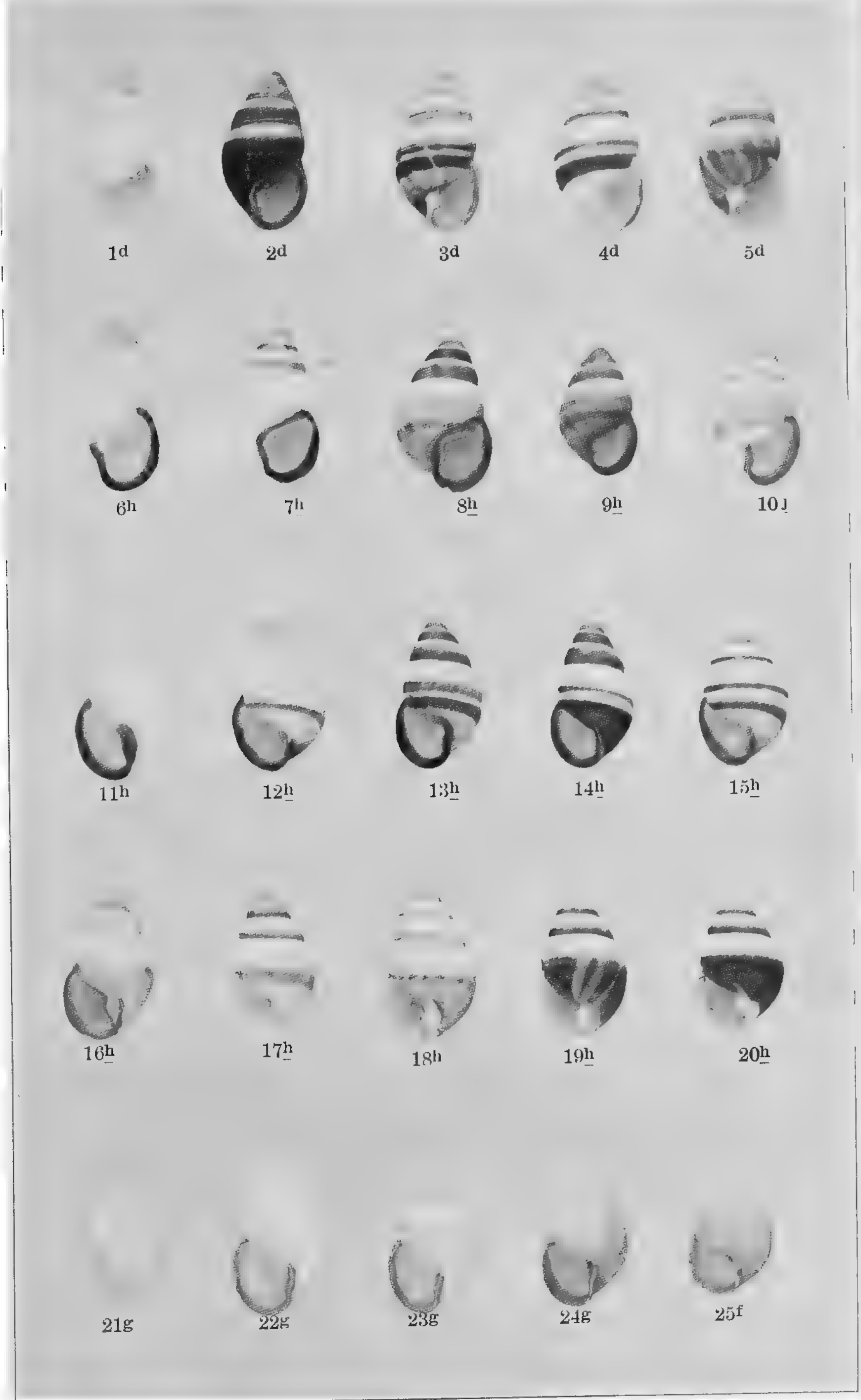
EIGHT GENERA OF ACHATINELLIDAE FROM FIVE ISLANDS

PLATE B.


MAP OF
OAHU
HAWAIIAN ISLANDS
Scale
0
5
10 miles
Kahuku Pt.
Laie Bay
Laie Pt
Kahana Bay
KANEOHE BAY
Mokapu Pt.
Kailua Bay
Waimanalo Bay
Makapuu Pt.
Kawaihoa
Waialae Bay
Kapahulu
Diamond Head
HONOLULU
PEARL HARBOR
Keahi
Barbers Pt. (Laeloa)
Kaneilio
Pokai Bay
Mauna Lahilahi
Kaena Pt
Waialua Harbor
Kaiaka Bay
Waimea Bay
Waimea R.
Anahulu R.
KOOLAU
KOOLAUPOKO
KONA
WAIALUA
EWA
WAIANAE
M.
W.
158°00'
157°40'
21°15'
40'
35'
30'
25'
20'
15'
10'
05'
55'
50'
45'



DISTRIBUTION OF TWENTY-FIVE SPECIES OF ACHATINELLA
FROM TEN VALLEYS



1d 2d 3d 4d 5d

6h 7h 8h 9h 10j

11h 12h 13h 14h 15h

16h 17h 18h 19h 20h

21g 22g 23g 24g 25f

VARIATION AND INTERGRADING OF FOUR SPECIES OF BULIMELLA

LETTERS USED ON PLATE B, TO DESIGNATE THE VALLEYS AND DISTRICTS ON THE ISLAND OF OAHU.

a, Waialei
b, Pupukea.
c, Waimea.
d, Kawailoa.
e, Opaiula.
f, Helemano.
g, Wahiawa.
h, Ahonui.
i, Kalaikoa.
j, Waipio.
k, Waiawa.
l, Ewa { Waimano.
Waimalu.
m, Halawa.
n, Moanalua.
o, Kalihi.
p, Nuuanu.
q, Pauoa.
r, Makiki.
s, Manoa.
t, Palolo.
u, Waialae.
v, Wailupe.
w, Niu.
x. Keawaawa.

a, Kahuku.
b, Malaikahana.
c, Laie.
d, Hauula.
e, Kaliuwaa.
f, Waiolu.
g, Punaluu.
h, Kahana.
i, Keawa.
j, Hakepuu.
k, Waikane.
l, Waiahole.
m, Kaalaea.
n, Kahaluu.
o, Heia { Ahuimanu.
Ioleka.
p, Kaneohe.
q, *r*, *s*, Kailua { Pohakunui.
Olomana Peak
t, *u*, *v*, *w*, Waimanalo.

M, Mokuleia.
L, Lehui.
W, Waianae.

[Italic letters in the second column are to be regarded as the equivalent of the underscored letters on the map.]

CHAPTER V.

THE FOUR SEGREGATIVE PRINCIPLES.

I. The Need of a Nomenclature Distinguishing between Racial and Habitudinal Segregation.

1. *The Interaction of Acquired and Inherited Characters.*

The interaction of the factors producing racial segregation and those producing social or habitudinal segregation should, I think, be clearly recognized, and a suitable nomenclature used for presenting the same. Increasing attention is being given to this interplay of influences; but clear expression of the relations of the factors is constantly obscured by lack of terms for designating the processes of segregation relating to acquired characters or habitudes.

In my paper on "Intensive Segregation" I emphasize the importance of the forms of *reflexive selection* "due to the relations of the members of the same species to each other, and liable to change without any change in the environment," and of *active* (*or endonomic*) *selection* "due to change in the successful use of the powers of the organism in dealing with the environment." In another paragraph I say: "Diversity in the uses to which different sections of one species put their powers when appropriating resources from the same environment must produce diversity in the forms of variation that are most successful in the different sections. This I call *active selection* as contrasted with *passive selection*, which varies according to differences in the environment. All diversities of environal selection that do not vary according to differences in the environment must be classed as diversities of active selection, for they must have originated in some variation in the powers of the organism, or in the diversity of uses to which it has put its powers."* The power of the organism to determine *industrial segregation* is considered in my paper on "Divergent Evolution," read before the Linnean Society in 1887.

In 1896, Professors Baldwin, Osborn, and Lloyd Morgan were independently led to consider the influence of individual powers of accommodation in enabling representatives of a species to survive in an environment that would otherwise be fatal, and so "giving time to the species to develop coincident variations (*i. e.*, congenital varia-

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* See Appendix II, Section I, 8, (4) and (18).

tions in the same direction),"* which are gradually accumulated by selection. Another point presented by the same writers is the continuity of tradition, secured by training, suggestion, and example on the part of the parents and imitation on the part of the young. The effects of tradition have also been very clearly illustrated by F. W. Headley in his recent book.† I quote a few sentences in which he summarizes the effects of accommodation and tradition:

> The result is that among the higher plastic classes of animals evolution proceeds more rapidly. But obviously the quickening up of evolution is not all. The individual gains in importance. He improves his powers, is able to face a change of environment that otherwise would have been fatal. He makes an environment for his young in which intelligence can be developed; he chooses the environment which they shall have when out of the nursery, and so decides to some extent what qualities shall be the winning qualities in life. In fact, he is beginning to take the helm and steer the species. Or we may put it in this way: When the individuals of one generation decide the environment in which the next shall grow up, selection ceases to be purely natural; it is in part artificial.‡

These quotations are sufficient to show that there is increasing recognition of the fact that there may be changes in the organism that are not dependent on changes in the environment, and are therefore not dependent on change in the form of the *natural selection*. In choosing terms for designating these processes I think we should carefully follow Professor Baldwin's suggestion "that selection in the Darwinian sense should be used only when the essential conditions of organic progress by survival are present, namely, variations and physical heredity."§

In my own usage, selection has been applied only to processes securing the survival of part of the variations of a race or species with the exclusion of other variations, and so influencing its powers of heredity; and isolation has been limited to the prevention of free crossing between co-existing groups. In order to do this, and at the same time clearly present the principles controlling the evolution of habitudes, it has been necessary to find two terms that might hold the same relation to innovation and tradition that selection and isolation hold to variation and heredity. The best words I have found are election

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* See letter from J. Mark Baldwin in Nature for April 15, 1897; also the same in Science for April 23, 1897, on "Organic Selection." In this letter will be found references to discussion on the subject during the previous year in various books and journals.

† Problems of Evolution, pp. 120–128. London, Buckworth & Co., 1900, and New York, Crowell & Co., 1901.

‡ Problems of Evolution, p. 128.

§ See Science May 8, 1898. The same limitation is also advocated in his Social and Ethical Interpretations, Appendix B.

and partition. The need of such terms will, I am sure, be recognized by many, though some may not consider the words I have chosen the best.

2. *Segregation is a Fundamental Law in the Organic World.*

One sphere in which it operates is racial (or aptitudinal) segregation, produced by the intergeneration of individuals with like innate characters. Another sphere is social (or habitudinal) segregation, produced by the association with each other of individuals with like acquired characters. *Segregate generation* (*i. e.*, the generation of like with like), *is a condition on which the present structure of the organic world depends.* Without segregate generation the differences of races, species, genera, and the higher groups could never have arisen, and if it were possible that it should cease, all these distinctions would ere long be obliterated. The fact that race characters are hereditary renders it certain that freely intergenerating races will, in a few generations, become one race. But the fundamental nature of the organic world is such that the only cases in which the law of segregation can be broken down are those in which the divergence is comparatively small. When amalgamation takes place it is usually varieties of the same species that unite. When physiological incompatibility has once been fully established, the segregation is never broken down; but, on the other hand, as long as there is any plasticity in a race, it is possible that new segregations may be introduced and one race divided into two or more races.

Having observed that segregate generation is the fundamental principle by which the world of sexually reproducing organisms is maintained, and having discovered that the art of breeding, by which the multitude of domestic races has been produced, rests on the control of segregate breeding, we propose to make careful investigation of the different forms of control influencing this principle and of the effects thus produced.

As an equivalent for segregate generation (or the breeding of like individuals with like), Romanes has proposed the term "homogamy." An objection to its use in this meaning is, however, found in the fact that in botanical language the same term has a somewhat different meaning.

It should be noted that this statement concerning the breeding of like with like does not imply that creatures freely mating with each other are entirely free from differences. Of multicellular organisms no two were ever found to be exactly alike; if, therefore, there is any mating of these creatures, it must be the mating of creatures that are not completely the same, either in structure or function. The point is that the greatest difference existing between any form of organisms and any other form that is capable of crossing with it, is very small compared with the differences presented by the vast world of organisms that are incapable of crossing with it. Cross-fertilization secures the blending of elements from individuals that are more or less divergent; but the degree of divergence that may exist without resulting in sexual incompatibility, either physiological, morphological, or psychological, is very small compared with the divergences that lie beyond the limits of compatibility. Again, we find that in some cases species incapable of crossing are so similar in visible characters that the naturalist finds difficulty in distinguishing them.

3. *Segregate Association,* a Fundamental Law on which the Social Structure of Each Species that is not wholly guided by Instinctive Aptitudes must rest.*

The necessity of a common language for a social group will be recognized by all. There must be a system of signs or signals by which the members of one group may call to each other when they wish to come together, may warn each other of approaching danger, and may in other ways coöperate in securing the sustenance, protection, and propagation of the group. If these signs are not instinctively made and instinctively understood, they must depend on suggestion, training, and imitation; and this suggestion, training, and imitation is made possible by the association maintained by the social group. It is a universal fact that the social characteristics of individuals of the same associating group are gradually unified by association. Again, it is certain that a group of freely associating and freely intergenerating individuals of different races of mankind will in time become assimilated in language, manners, and customs, and finally in race, however different they may have been when first brought together. The blending of two strongly marked species is usually prevented either by instinctive aversion, by unfruitful crossing, or by the sterility of the hybrid offspring, as in the case of the mule; while the blending of two civilizations is liable to be prevented by the superior power of one completely overshadowing the influence of the other. Moreover as long as racial barriers are not broken down, distinctions of social types are not often wholly obliterated. This is naturally the case as long as the training of the young, and so the transmission of tradition, remains chiefly with the parents.

Segregate association, that is, the association of like with like, is the fundamental factor in the production of habitudinal segregations;

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* That is, the association with each other of individuals with like acquired characters.

and, as will be more fully explained in another chapter, it is brought about by the coöperation of habitudinal demarcation through partition, and habitudinal intensification through election. The methods of this election are first through the different forms of approval and disapproval used in training the young, and second through the promotion and wide influence given to individuals attaining the highest recognition of public opinion and the suppression of individuals falling below the lower limits set by the laws and customs of the community.

Divergent forms of civilization can neither be established nor maintained without the continuous operation of segregate association.

For designating the effects of segregate association I often use the term "habitudinal segregation" rather than "social segregation," because in creatures entirely guided by instinct there may be elaborate forms of social organization, and therefore forms of social segregation, that rest mainly, if not entirely, on racial characters produced by racial segregation; while under "habitudinal segregation" I wish to consider the evolution of acquired characters under the operation of segregate association. If ants and bees learn by training and imitation incorporated in traditions, then the growth of their social organizations should be treated under this department of segregation; but, if not, then their evolution, both physical and social, comes under the department of racial segregation.

4. *The Interaction of Racial and Social Evolution must be considered.*

The interaction of racial and social (or habitudinal) evolution and the exposition of the laws regulating the same, by which man is to gain control of his own evolution, is the broad sphere in which the biology and sociology of the future will expand. Ward, Giddings, Baldwin, and other Americans are exploring this field, and in Europe the trend is in the same direction, if I judge rightly. The nomenclature which I propose and illustrate in the following pages will, I think, aid in discussing the problems of biology and sociology that are now coming to the front. I should not have had the patience and courage to attempt to present a scheme for so wide a field if I had not seen the pressing need for such a method from the side of biology. I also believe it will be a great advantage for sociology if a harmonious and correlated nomenclature can be brought into use in both biology and sociology. Some sociologists, recalling the nomenclature and exposition introduced by Herbert Spencer on the basis of an assumed correspondence between the biological and the social organism, will instinctively shun the use of a terminology that suggests a correspondence and interdependence between the two spheres of evolution. There will, however, be others, who have come into sufficiently close contact with the problems of evolution, in both realms, to realize that great illumination for each will be found in the study of the interaction between the two realms. Those who are doubtful concerning the interaction of the two spheres will gain light from Baldwin's Social and Ethical Interpretations and his Development and Evolution, and from the discussions on organic selection given by Osborn, Baldwin, and others in Science and The American Naturalist during 1896–98. A clear exposition of "organic selection" is also given in Conn's "Methods of Evolution," a work presenting with remarkable fairness the results reached by different schools of biologists, and the same subject is discussed by Lloyd Morgan in his volume entitled "Habit and Instinct," especially in the last four chapters.

5. *Determinate Evolution of Evolutionary Terminology.*

With gradually advancing clearness, the relations of the two spheres of evolution to each other have been recognized, while at the same time the necessity for a distinct nomenclature for the processes shaping the evolution in each sphere has been increasingly realized and in some degree provided for. On the one hand variation, heredity, and adaptation have been restricted in their application to processes and powers by which racial characters are produced, and on the other hand the correlative terms "innovation,"* "tradition,"† and "accommodation"‡ have been introduced to designate analogous processes by which acquired characters are produced. There remains, however, much confusion due to attempts to extend the scope of the term "selection" so as to include the processes by which social habits and customs are established; and sometimes even to designate processes that properly come under the term "isolation." I believe the only remedy will be found in the introduction of two terms that shall take the place in the theory of the evolution of habitudes that isolation and selection fill in the theory of the evolution of aptitudes. The advance toward this end is, I believe, an evolution that can not be stayed. What terms will eventually prevail is a matter of less certainty and of less importance.

The scheme presented in this chapter is offered by way of suggestion and with the hope that it may lead to suggestions from others, and thus help in the attainment of a completer theory and better nomenclature than any now in use. As has been said by Prof. E. O. Whitman, "Cross-fertilization works rejuvenation in theories as in organisms."

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* See Tarde's Social Laws, pp. 40, 52.

† See Baldwin's Development and Evolution, p. 152.

‡ *Ibid.*, p. 151.

II. Segregation the Combined Result from Four Principles.

1. *Racial Segregation Controlled by Two Principles, and Habitudinal Segregation by Two.*

Racial or aptitudinal segregation rests on heredity and variation, and is controlled by segregate intergeneration of individuals according to their inherited characters; while social or habitudinal segregation rests on tradition and innovation and is controlled by segregate association of individuals according to their acquired characters. The control of variation and heredity rests directly upon the limitations of segregate intergeneration produced by the two principles, racial demarcation through *isolation* and racial intensification through *survival* (in its two forms, selection and indiscriminate elimination). The control of tradition and innovation rests upon the limitations of segregate association produced by the two principles, habitudinal demarcation through *partition* and habitudinal intensification through *success* (in its two forms, *election* and indiscriminate failure). We have, therefore, four main principles coöperating in the production of segregate types, namely, partition, success, isolation, and survival. In order to understand the evolution of sexually reproducing organisms it is necessary to gain clear conceptions of these four principles and of their relations to each other in producing the ramified and intensified segregation of types. Each of these principles when called into action has more or less influence on the control of segregate generation, and, therefore, influence on the types of the organism.

2. *The Importance of Isolation.*

The importance of isolation as a coördinate factor with selection in the evolution of species is now gaining wide recognition. Romanes' exposition of the subject, given in Darwin and After Darwin, Part III, is so convincing that an increasing number of English and American biologists are disposed to grant the general soundness of the claim that the prevention of free crossing is a necessary principle in the divergent evolution of races and species; but some of the same writers are not satisfied with the nomenclature which Romanes has adopted in setting forth the doctrine. In the first place, he fails to discriminate clearly between selection and isolation. This has, I think, arisen from following the custom of describing any influence that tends to transform species as a form of selection. Following this method, Karl Pearson defines sexual selection as including "all differential mating due to taste, habit, or circumstance which prevents a form of life from freely intercrossing."* Following the same method Ro-

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* See Grammar of Science, p. 417

manes says of infertility between varieties of the same species: "For the sake of convenience, and in order to preserve analogies with already existing terms, I will call this principle physiological selection or segregation of the fit."* Since the publication of his essay on Physiological Selection in 1886, and of my papers on Divergent Evolution and Intensive Segregation in 1887 and 1889, isolation has by general consent come to mean *the prevention of free-crossing between groups existing at the same time.* In accordance with this usage, in Darwin and After Darwin, Romanes often substitutes physiological isolation for physiological selection, which is a great gain. When, however, he gives a precise definition of isolation, he extends its meaning so as to include the prevention of crossing between those members of the group who succeed in living and propagating and those who die without propagating. This definition of isolation makes it include natural selection as one of its many forms. (See Darwin and After Darwin, Part III, pp. 9, 10.) I recognize most fully the importance of keeping in mind the fact that natural selection would have no power to transform species if it did not prevent the crossing of the fit with the unfit; but I think the relation of the different factors can be best presented, first, by restricting the term "selection" to the influences that determine the survival (that is, the continued propagation) of the fit innate variations of any given group, and the elimination (that is, the disappearance) of the unfit, thus preventing the crossing of the fit with the unfit; second, by restricting the term isolation to the prevention of free crossing between groups existing at the same time; and third, by showing how these two principles coöperate in producing racial segregation of the fit which is the essence of racial evolution. The conception of racial evolution which I thus expound is much the same as that presented by Romanes; but, if I mistake not, the meanings which I attach to the different terms are in better accord with general usage. I also attempt a wider problem, in that I now add to my exposition of racial segregations and amalgamations a similar analysis of habitudinal segregations and amalgamations, with the special purpose of bringing clearly into view the action and reaction between the two spheres of evolution. I think that even the most conservative biologists are coming to recognize with Mr. Headley that the racial evolution of the higher animals, and especially of man, is guided by their social evolution (or by their *progress*, as he would put it), while many already agree with him in his statement that "If natural selection works without isolation, only monotypic evolution can result."†

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* Journal Linnean Society, Zoölogy, Vol. XIX, p. 354.

† See Problems of Evolution, pp. 128, 175.

3. *Definitions of the Four Segregative Principles.*

First. *Partition* is the setting of individuals in groups, the members of each group associating with each other and securing what Professor Giddings calls "socialization," and what Professor Baldwin calls "social generalization," through learning from each other.

Second. *Success* (of which election is the discriminate, and, therefore, the more important form). Election is the superior influence of such individuals as have best attained the ideals, habitudes, and acquired characters fitting them for individual success and leadership; and the inferior success and influence of those that are deficient in the same ideals, habitudes, and acquired characters. The term "imitative selection" has been defined by Professor Baldwin as produced by "imitative propagation from mind to mind with social heredity"; and as resulting in "survival of ideas in society."* Imitative selection seems, therefore, to cover, at least in part, what I call election. I have not, however, been able to use it in the analysis given in this chapter; for in my tables selection is applied only to factors determining the survival of innate variations, and, therefore, influencing racial heredity. The indiscriminate form of *success* I usually call indiscriminate failure; for it is most effective in producing divergent types when indiscriminate slaughter, or absorption by a more powerful race, leaves only small and isolated fragments of the original type of civilization.

Tarde emphasizes the importance of "the suggestive and contagious influence of certain select individuals upon the group as a whole."†

Third. *Isolation* is the setting of individuals in groups, the members of each group intergenerating, and so securing racial generalization (or fundamental unity of inheritance) within each group, while between the groups there is prevention of free crossing.

Fourth. *Survival* (of which selection is the discriminate, and, therefore, the more important form). Selection is the survival (that is, the continuance from generation to generation) of those individuals whose innate characters give them the advantage over others in coming to maturity and reproducing. It avails nothing in selection for individuals to complete their normal term of life, unless they leave offspring in due proportion; and numerous offspring avails

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* See Appendix B, Social and Ethical Interpretations, 1897; also *Science*, November 19, 1897, p. 770; also Development and Evolution, 1902, p. 166.

† See "Social Laws," p. 46 of the translation published by The MacMillan Co., New York.

nothing in determining selection unless they have power to live and reproduce. The indiscriminate form of survival I call "indiscriminate elimination." It is often the chief principle by which divergence is initiated in two or more isolated masses of a species. If indiscriminate destruction reduces each group to but one or two individuals capable of propagating the race, divergence immediately arises in regard to one or more points of character.

Partition, acting on acquired characters, produces habitudinal demarcation with *initial habitudinal segregation.*

Election, acting on acquired characters, produces *intensified habitudinal segregation.*

Isolation, acting on inherited characters, produces racial demarcation with *initial racial segregation.*

Selection, acting on inherited characters, produces *intensified racial segregation.*

Partition and election acting together produce cumulative habitudinal segregation.

Isolation and selection acting together produce cumulative racial segregation.

Partition and isolation acting together produce typal demarcation with initial segregation, both habitudinal and racial.

Election and selection acting together produce intensified segregation, both habitudinal and racial.

The four principles acting together produce allogamic evolution, both habitudinal and racial, through the segregation of types.

4. *Objections that may be Raised to the Terms Used.*

It may be thought that such terms as "partition" and "election" are not needed in the exposition of the process of evolution; that the whole process may be considered as due to selection, and, if influences not recognized by Darwin are discovered, they should be designated as forms of selection. My suggestion is that a definite attempt to construct a nomenclature, enabling one to set forth the evolution of acquired characters and the influence of the same on the evolution of inherited characters, will show the investigator that great gain in brevity and clearness may be secured by the use of separate words to designate the principles in habitudinal segregation that correspond to isolation and selection in racial segregation. But, even if the need of such terms is recognized, objection may be raised against the use of the term "election," on the ground that it properly signifies the elevation of an individual to a position of influence by his winning the conscious choice of rational beings, while in the nomenclature here proposed it is made to cover superior influence over the acquired characters of associates, whether the community consists of rational beings or not. A similar objection has often been urged against the use of "selection" in the Darwinian sense; but, on the whole, no better word has been found to designate the gaining of a full share in the propagation of the next generation, and so a full share of influence on the inherited characters of the community, whether it be by winning the interest of the rational part of the environment or by securing adaptation to other conditions in the environment. Each new term is an innovation, and like all innovations must prove its usefulness before it can prevail or be elected.

III. INTERACTION OF THE FOUR PRINCIPLES OF SEGREGATION.

1. *Increased Effects Produced by the Repeated Action of One Principle or the Combined Action of More than One.*

Mr. Headley says that, in my terms "intensive segregation" and "cumulative segregation" the words "intensive" and "cumulative" are "misapplied." (See Problems of Evolution, p. 178.) I think his criticism is chiefly due to his having failed to note the definitions I have given to the terms and the way in which I have applied them. Intensive segregation I have described as due to natural selection and the other principles, producing transformation when coöperating with isolation.* Cumulative segregation is due to a succession of isolations coming at long intervals, in which each isolation opens the way for the formation of some new habit shaping the method of dealing with the environment, and, therefore, leads to the formation of a divergent species. For example, if a variable species of snails, having but little opportunity for transportation beyond the limits of the valley it inhabits, and no power for migration beyond the same, finds its habitat in the groves at one end of the chief mountain range of the island of Oahu, it may become well adapted to the conditions before a branch colony is planted in the next valley. Though the vegetation is the same in the two valleys, the new colony may be started by a single individual, whose habits lead it to prefer, for food and shade, some species of plant that is but little used by the mother colony, and thus divergent forms of endonomic selection shape the two colonies into two species. After many years the transportation of an individual from the second colony may result in the planting of a third colony with still further divergent habits; and so on till the valleys at the opposite end of the mountain range have become the habitat of species very closely re-

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* See Appendix I, Section VII, 3; also Appendix II, Section I, 8.

lated to each other, but quite distinct from the mother species from which they have been separated by many successive isolations.

Mr. Headley recognizes that there may be change in the species without change in the environment in what he says concerning "*alternative methods of adjustment to the same environment*" (p. 149). He illustrates this in the following way: "For many butterflies, birds [that prey upon them] are an important part of the environment. They may adjust themselves to it (1) by developing great powers of flight, or (2) an offensive taste, or (3) they may 'mimic' another nauseous species, or (4) come to resemble some such thing as a dead leaf and so be protectively colored" (pp. 147, 148). This power which is here recognized by Mr. Headley as belonging to many species fully justifies his statement that "Often there is a variety of possible adaptations to one and the same environment" (p. 146). How, then, can he defend the following sweeping generalization given by him in many passages, on widely separated pages? I will quote only two or three. "If the environment remains unaltered, evolution ceases. * * * Further evolution can take place only if an environment that is in some way different offers itself" (p. 103). "Each successive step of evolution is due to some change in the environment" (p. 111). "Nothing but change of environment can lead to further evolution" (p. 153).

Notwithstanding this inconsistency in his interpretations, he gives us many fresh and interesting facts.

2. *Importance of Each of the Principles.*

It is not easy to determine whether each and all of these four principles began to control evolution from the very dawn of life; but when once fully established we find them coöperating in such a way that it seems impossible to overestimate the importance of each in its own sphere of action. It is now generally recognized that monotypic evolution, that is, the transformation of any single type into a succession of forms through which it gradually passes without branching, is largely due to selection; but, in a world where two or more species exist, even in the case of monotypic evolution, the whole process is also dependent on isolation; for if the single type under consideration freely crosses with other types, it loses its separate identity. In a world of diverse types the monotypic evolution of any one type is, therefore, necessarily a process of intensive segregation, in which isolation and the principles producing transformation (of which selection and election are the chief) coöperate. Since sexual reproduction began heredity has been controlled by the segregate generation of individuals according to their innate aptitudes for adaptive response; and isolation and selection have coöperated in producing segregate generation, and so in intensifying the aptitudes. What, then, shall we say of the segregate association of individuals according to their habitudes, acquired by experimental initiation, individual repetition, social imitation, and other methods of accommodation opening to the different groups divergent methods of dealing with the environment; and what of the partition and election which coöperate in producing the segregate association, and so in intensifying the acquired adjustments? Did the individuals of the primitive form or forms of life possess powers that were in any way or in the least degree discriminative? Had they any power to select that which is needed and to reject that which is useless or detrimental? And when the environment became somewhat complex, had the same species power to divide, one section establishing close relations with one part of the environment and another section with another part of the environment? If the correct answers to these questions are in the affirmative, then from early times habitudinal segregation, in its two forms, partition and election, have had an important influence on racial segregation, and, therefore, on the evolution of innate aptitudes.

In the production of segregated racial types isolation seems to be the most essential of the four principles, for there can be no racial segregation where there is no isolation, while there may be cases of segregation and divergence (at least for a number of generations) that are not at all dependent on new methods of action of any one or more of the other three principles. Such a case occurs when some peculiar variation or mutation, being transported to a position where there is no opportunity of crossing with other varieties, propagates its own peculiarity for many generations, though exposed to the same external conditions as the body of the species from which it has been separated. If, however, the isolation is continued through a long series of generations, new forms of selection inevitably arise, and in time new forms of acquired character resulting from new forms of activity and new forms of direct stimulus from the environment; and in this way the initial segregation produced by the isolation is intensified by diverse forms of selection and by modifications resulting from established habits. Moreover, the acquired characters may become the active agency leading to new groupings of individuals, and in many cases these new groupings introduce, or are accompanied by, groupings according to natural aptitudes and other innate endowments. In other words, using the terms just indicated, we start with isolation, which opens the way for divergent forms of selection, and the new forms of selection lead to new forms of partition, and these lead to new forms of isolation, thus establishing a circle of influences. Again, new forms of partition open the way for diverse forms of election, which result in the success of divergent habitudes in the separated groups; and these divergent habitudes may bring the individuals to whom they belong into positions producing isolation, and into divergent methods of dealing with the environment, and so subject them to divergent forms of selection producing divergent racial evolution.

We therefore observe that, in the evolution of the higher types of animals, each of these four principles must have a most important part; for, in producing divergent racial types, isolation is absolutely essential, and partition is the forerunner preparing the way for isolation. Again, selection usually operates in each generation, either in giving emphasis and stability to types already attained, or in molding the separate groups created by partition and isolation, according to new necessities, which are, in most cases, introduced by the new experiments, new attainments, and new habitudes that have been established by the different forms of election. My interpretation of these factors does not tend toward the minimizing of the importance of selection; but it shows that isolation, partition, and election are of equal importance in their own spheres. It shows that the transformation of forms that do not freely intergenerate is always more or less divergent, and that the racial divergence of any two forms is absolutely dependent on isolation, *i. e*, the prevention of free crossing. It further emphasizes the fact that selection, both in its reflexive and its environal forms, is in a large degree controlled by the varying habitudes and aptitudes of different sections of a species, so that the isolated portions of a variable species would in time develop different forms of selection, even if they could be exposed to absolutely similar environments. These points are all presented in full in the paper reproduced in Appendix II, but the new nomenclature here introduced facilitates our apprehension of the facts.

3. *The Two Methods of Generalization.*

Racial generalization is produced by heredity with free crossing within the bounds of each racial group. *Habitudinal generalization* is produced by tradition with free association within the bounds of the social group. The influence of heredity is so fully recognized that we need not stop to illustrate the fact that two or more somewhat divergent types, when freely intergenerating for many generations, will be reduced to a single racial (or aptitudinal) type which is perpetuated with considerable constancy from generation to generation. It is also manifest that tradition, which transmits the habits of each generation to the next, through the training and suggestion given by parents to their offspring and by the experienced leaders to the multitude, and responded to by the instinct for imitation possessed by the young and inexperienced, will establish and perpetuate a more or less constant social, or habitudinal, type. And it should be especially noted that the habits thus transmitted from generation to generation determine the relations of the group to the environment, and, therefore, the form of selection that continues with cumulative results in successive generations. The influence of habitudinal generalization is illustrated by the following case:

4. *Change of Tradition in the Case of the Chimney Swift.*

The chimney swift of eastern North America, often called the chimney swallow, has made an important change in its habits since the settling in this region of Europeans who build houses with chimneys. We know that before the coming of the European the traditions of this bird determined that hollow trees should be occupied as the appropriate places for their nest-building. How the present tradition, giving the preference to chimneys, was started, we are not informed; but we may believe that a pair of birds of an investigating spirit, finding that the hollow trees in which they and their ancestors had been in the habit of building had been cut down, ventured to make the new experiment. Being rewarded with success, election is on their side, and their descendants survive to perpetuate the habit. Other birds of the same species see their success and follow their example; and as chimneys are multiplied, while hollow trees are diminished in number, the followers of the new habit in time outnumber the adherents to the old tradition, and from that time on the old conservative habits crumble rapidly away. The vast majority of the species have now abandoned the old tradition, and the newer tradition now prevails everywhere, except in the Dismal Swamp (a region about 30 miles in length and 10 miles in width, in the States of Virginia and North Carolina), where their unconscious helper has failed to erect his chimneys.

5. *The Two Methods of Adjustment.*

Aptitudes are inherited forms of adaptation resulting from tentative variations accumulated by the survival of the fittest. Habitudes are traditional accommodations (that is, traditional forms of adjustment), resulting from tentative innovations accumulated by repetition and imitation of successful experiments.

Adaptation in plants and in the lower types of animals is gained chiefly by *variation* in the degrees of innate qualities and in the intensity of innate activities, molded in successive generations by the survival of individuals having the fittest endowments in each isolated group. This molding of variation and heredity by isolation and selection results in racial segregations. But even plants are endowed with powers that enable each individual to do something toward directly adjusting itself to the environment in which it is placed, for they will stretch their branches and turn their leaves toward the light, and their roots will bend toward moisture and away from hard or irritating substances obstructing their course. This power of the individual for experimental action with ability to persist in the action that secures the best results is called *accommodation;* and the molding of accommodation and tradition into habitudes produces habitudinal segregations with their adjustments. We find that accommodation fills a sphere of increasing importance in the evolution of animals according to the degree of their mental endowments. In studying the evolution of the higher animals it is especially necessary to consider the adjustments produced through the molding of accommodations by election, as well as those produced by the molding of variations by selection. The importance of prolonged infancy and childhood in mankind has been rightly emphasized by John Fiske; but the significance of this condition is found in its opening the way for the building of habits guided by the experience of many generations. The combined wisdom of countless ancestors thus is transmitted to the young through language, example, and training, formulated in maxims, and customs, in penalties and rewards, and instilled into minds specially endowed with powers of imitation and with aptitudes for forming lasting habits; and the process is continued much longer than in the case of animals lower than man. In the case of beasts and birds the equipment for the struggle of life is received in a larger degree through inherited powers and instincts, though tradition is also of importance.

6. *The Two Methods of Adjustment as Applied to New Conditions, Suddenly or Gradually Encountered.*

I have already considered certain cases involving resources that are varied but familiar to the species and easily explored, in which habitudes (that is, traditional forms of accommodation), and aptitudes (that is, inherited forms of adaptive variation), become the controlling factors in determining selection. We wish now to consider cases in which the new environment fails to present the conditions and resources to which the organism has been accustomed. In the first place, if the species has but slight accommodative power, and the new conditions are suddenly encountered, habitudes and aptitudes will be of little or no avail in guiding; and, though some of the variations may be able to battle with the new conditions for a generation or two, none will be able to survive and propagate permanently.

In the second place, if the new conditions are slowly introduced, as is often the case in geological changes, innate variation, combined with high reproductive powers, may enable them to meet the changes as well as do those endowed with much higher powers of accommodation; but in cases of sudden change, high powers of accommodation will often preserve the group from extinction till time has been given for the accumulation of what Lloyd Morgan has called "coincident variations."* When accommodation thus opens the way for successful selection, Professor Baldwin calls the process "organic selection." I am disposed to raise the question whether the term "coincident variation," suggested by Lloyd Morgan, does not meet the case more exactly; and when the variations are accumulated, may it not be well to call the process "coincident selection"? Let it, however, be carefully noted that a slow change of conditions, either in the relations of the organism to the environment or in the relations of the individuals of the organism to each other, may result in the gradual transformation of slightly varying habitudes and aptitudes through election and selection, even when the range of individual accommodation is very small, and when the degree of variation in inherited qualities is not large, in any one generation.

7. *In the case of Civilized Man, especially when exposed to sudden change, Accommodation overshadows and controls all other influences:* (1) *by Organic Selection, that is, by giving time for the action of Natural Selection, and* (2) *by the success of Accommodation and Tradition, removing the need of special variation in order to survive.*

The great importance of accommodation is often seen in birds and mammals, and pre-eminently in man. The power of man to occupy every land, of every clime, that is not entirely devoid of vegetation, or continuously capped with ice, is due to his powers of accommodation. By accommodation he overcomes his enemies; by accommodation he wins nourishment in hitherto untried fields; by accommodation he protects himself against the extremes of heat and cold, to which he would soon succumb if fortified simply by the inherited characters of his body thus far attained, unaided by artificial clothing and shelter. But even in the case of man, who is able by his arts to adjust himself to great extremes of climate, there have arisen different races, with special adaptations to different climates in their inherited characters. If the average child of tropical Africa and the average child of Greenland should exchange homes and training, both would be heavily

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* See "Habit and Instinct" (London, 1896), pp. 312ff; also "Animal Behavior" (1900), pp. 39, 115; also Baldwin's "Development and Evolution," Appendix A.

handicapped in the struggle for life, through lack of innate adaptation. Man was probably fully adapted in constitutional character to warm climates before the arts of clothing and house-building had arisen; but we may well believe that these arts were found of the utmost importance when tribes began to invade the colder climates, or when cold weather invaded their native lands; and that it was in consequence of these arts that permanent colonies in the colder regions became possible. How then shall we account for the constitutional adaptations of the Eskimo race—adaptations extending even to the tissues of the body, so that they are incased with a layer of fat just beneath the skin, rendering the same kind of protection from the cold that the whale receives from his blubber?* It seems probable that we have in this case an illustration of the way in which accommodation prepares for, and leads up to, certain conditions producing selection. In the remote ancestors of the Eskimo, the habit of protecting from the cold by clothing and other arts undoubtedly preceded the establishing of the racial characters by which they are now in a measure protected; but the devices of the accommodating faculties were not sufficient to prevent those endowed with even slightly developed constitutional powers for withstanding the cold from enjoying some advantage in meeting the conditions of life, and so being gradually selected. If this is a true interpretation of the case, it illustrates what Professor Baldwin calls "organic selection" and Professor Lloyd Morgan calls "accumulation of coincident variations." The importance of this principle in preserving certain creatures, when subjected to heavy change within the period of any one generation, can not be questioned. The necessity for powers of accommodation in order to meet successfully great changes is of two kinds: First, for power to provide against great alternations in conditions that come to each generation, such as changes in temperature and changes in the degree of moisture; and second, for power to meet new sets of conditions, to which the race has, in its previous experience, never been continuously exposed. For the former of these classes of changes, many species of the lowest animals and large numbers of plants are as fully equipped as the higher animals, including man; but the nature of the equipment is, in the case of the plants, wholly physiological, and, in the case of

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* In "Greenland Icefields and Life in the North Atlantic," by G. Frederick Wright and Warren Upham, I find the following quotation from F. A. Cook, ethnologist of the first Peary North Greenland Expedition, concerning this character in the Eskimo: "The muscular outlines of the body are nearly obliterated from the fact that they have immediately beneath the skin a layer of blubber, or areolar tissue, which protects them against extreme cold."

the lower classes of animals, largely physiological, with some coördinated instincts; while in the case of man the power of adjustment is very largely psychological, and in the case of the other classes of animals, above the lowest, physiological and psychological adaptations constantly coöperate. The explanation of these inherited adaptations of the humblest organism to climatic and other conditions involving great fluctuations is, I think, to be found in the fact that they or their ancestors were gradually introduced to these alternations, and that selection has thus had an opportunity to work for countless generations in producing the corresponding complex adaptations and powers of accommodation. It may be granted that man and his ancestors have consumed an equal succession of ages in attaining the inherited intellectual constitution that fits him for his higher sphere, without lessening our apprehension of the wonderful contrast between man and all lower organisms, in his power to enter suddenly upon a new set of conditions. This power is so great that man may suddenly enter a new territory, furnishing not a single product that he can eat, and by his art of agriculture so completely meet his needs that he becomes a permanent settler without even subjecting himself to any new form of selection. *In other words, accommodation is in some cases so complete that coincident selection is prevented. This suggests that in some spheres of activity, coincident (that is, organic) selection, is less liable to occur in man than in animals whose accommodation is less complete.*

8. *Endonomic Selection illustrated by Several Species of North American Birds.*

By means of accommodation birds and beasts determine their relations to the environment, and so determine the kind of selection to which they and their descendants are thereafter subjected. The choice of conditions that have brought pleasant experiences and the avoidance of those that have brought unpleasant experiences is a degree of intelligence enjoyed by many species of animals, and is a form of accommodation that may determine the mode of life and so determine the forms of selection. For example, the cliff swallow, ranging over most of North America, has accommodated itself to the new conditions introduced during the past two centuries by the occupation of the country by house-building people. Except in a few of the Western States, where the population is sparse and the houses few, it has deserted the cliffs and taken up its abode under the eaves of the houses, thus bringing itself into very close connection with man and subjecting itself to some forms of selection which it might have escaped by remaining in the cliffs.* These forms of selection are imposed on itself by the forms of accommodation the species has assumed, for the conditions are not so determined by the environment that no alternative remains to the organism. The cliff swallow might still build its nest in the cliff. The selection to which it is exposed is determined by the choice of the bird between alternatives afforded by the environment, and may therefore be called endonomic selection.

9. *Endonomic and Coincident Selection Illustrated by the Survival of Infants Fed on Substitutes for Mother's Milk.*

Not only are previous forms of environal selection brought to an end by accommodation, but certain forms of reflexive selection may be thus made to cease, and perhaps other forms introduced. From the era when the mammalian class first arose till comparatively recent times, every mammalian mother that failed to give milk also failed of raising her young; and so the propagation of a stock seriously deficient in this respect was rigorously prevented by filio-parental selection. However, amongst human mothers such cases occasionally arise; and, amongst civilized races, the provision for the young thus deprived of their natural nourishment is so complete that they are placed at no disadvantage. This form of filio-parental selection, which has been in full force for countless ages, now ceases for civilized man. Among half-civilized races the substitutes for the mother's milk vary with each nation, and the original filio-parental selection is supplanted by a form of social selection; for the article used as a substitute is determined by tradition, and the material furnished is so deficient in the needed qualities that a proportion of the infants are unable to survive on such food. The survivors are, therefore, determined by endonomic selection. They are selected on account of their being better endowed for meeting the ordeal of feeding on the substitute provided by the tradition of the community. But it is also an example of coincident selection; for if accommodation had not come in to aid in the process all infants whose mothers failed to give milk would have perished. On

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* I am informed by Prof. Lynds Jones, of Oberlin College, that several birds of North America have passed through a similar transformation of their habits. Besides the cliff swallow just mentioned, which attaches its nest to the overhanging eaves of a house instead of plastering it against the roof of a cave or hole in the cliff, there is the barn swallow, which usually attaches its nest to the rafter of a barn, also the chimney swift (referred to in the early part of this section), that used to build in hollow trees. The tree swallow and the house wren are two species that are still in a transition state in their habits, for many of them avail themselves of bird-boxes or of holes and snug nooks about houses, while others prefer holes in trees and stumps, as in better accord with old and safe traditions.

Ponape, one of the Caroline Islands, the only substitute for mother's milk known to the aborigines is the juice that exudes from the immature fruit-stalk of the cocoanut tree when the end of the immense bud is sliced off. In Japan, if a wet nurse can not be provided, sweet extract of malt is used. In some lands mare's milk is used; in some ass's milk; and in others goat's milk, or cow's milk; but all these are somewhat deficient, unless modified and sterilized by the highest skill of the physiologist and chemist. *Any case of selection introduced and protected from failure by accommodation is a case of "coincident (or organic) selection."**

10. *Endonomic Selection and Coincident Selection Contrasted.*

Active (or endonomic) selection is due to powers enabling the organism to deal with the same environment in different ways. This power is especially manifest when the organism is dealing in isolated groups with the same conditions. Different methods arise:

(1) Because the innate aptitudes of different individuals and groups for dealing with the environment differ somewhat. This results in aptitudinal selection.

(2) Because the training, and, therefore, the habitudes, of different individuals and groups, in dealing with the environment, differ somewhat. This results in habitudinal selection.

(3) Because individuals with the same aptitudes and habitudes may take up different methods of dealing with the same environment, through the accidents attending their entrance on their new districts, both in cases when these new districts all differ from the original home in the same way and when all afford exactly the same conditions as the original home. Shall we call this accidental selection? Or will some one suggest some other term more suitable?

Coincident (or organic) selection is due to the protection derived from the discriminative and other accommodational powers of the individuals, preserving the organism from extinction under the stress of great and sudden change, either in the environment or in the relations of the members to each other, and thus giving time for the production and accumulation of variations that coincide with the accommodation in adapting the organism to the new conditions.

Active (or endonomic) selection rests on "alternative methods of adjustment to the same environment *till the organism has adopted a particular method of suiting itself to its conditions.*"†

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* See Baldwin's Development and Evolution, pp. 95 and 173.

† This form of statement is quoted from Headley's Problems of Evolution, p. 149, where he is describing what he calls methods of evolution by natural selection.

Coincident selection rests on the protective and, therefore, controlling influence of *accommodation* rather than *adaptive variation*, during several generations of first encounter with great changes.

11. *Coincident Election Illustrated.*

Any form of election when introduced and protected from failure by variation and selection I call "coincident election." A ship bearing a number of families of Europeans is wrecked on an island of the central Pacific, where the only land product available for food is the cocoanut, while the sea is swarming with fish, sea-weeds, crabs, shellfish, etc., furnishing a large variety of nourishment. One-half of the shipwrecked people are by nature fond of the water and are able to secure an abundance of food. The others, unable to swim and dreading the sea, seek their support from the barren land and are so hard pressed for food that most of them perish, while some of them overcome their instincts and seek food from the sea, though at a disadvantage as compared with those who are at home in the water. In time the arts of fishing, and swimming, and diving, and canoe building and navigating are so fully developed that a thrifty and vigorous colony is established, in which the type of election, both reflexive and environal, is determined by the relations of the community to the sea. But these relations to the sea were made possible by the fact that part of the community were by nature endowed with some measure of aptitude for such a life. If all had been as destitute of such aptitudes as a colony of gorillas the whole colony would have perished, unless perchance a few might have led a precarious existence, subsisting entirely on cocoanuts. *Such a case would be an example of coincident election.*

12. *Endonomic and Coincident Influences Contrasted and Defined.*

Isolation, selection, partition, and election are controlled by endonomic influences when the relations of the group to the environment are liable to be turned in different directions according to the previously attained innate aptitudes or acquired habitudes of the individuals from whom the colony springs. This action becomes most manifest when the isolated sections of the group are exposed to the same environment that surrounds the original stock; but there may also be alternative methods of dealing with a new or greatly changed environment, and in such cases endonomic influences are present.

If inherited aptitudes are the controlling influence preceding and shaping the habitudes, then the partition and election are said to be coincident. If acquired habits and other powers of accommodation are the controlling factors, then the isolation and selection are said to be coincident. It therefore follows that in the lower forms of animal life the partition and election is largely coincident, while in the case of the higher animals, and especially with man, the powers of accommodation being the leading factors, the isolation and selection are largely coincident.

Industrial partition brings together, in the mining regions of Colorado, a peculiar type of people, gathered together from many regions where the opportunities for exercising their special training are not as great as in this frontier mining region. But this industrial partition introduces and determines industrial isolation, for it inevitably leads to the segregate propagation of the peculiar type brought together in these mining regions; and this industrial isolation thus produced is an example of *coincident isolation.*

Active (or endonomic) influences are due to the fact that the species may use alternative methods. The number of alternative methods of dealing with the environment rests upon the variety of possible choices open to the different sections of a species; and this is determined by the variety of innate aptitudes and of acquired habitudes, and of new discriminative experiments that the species can furnish.

Coincident influences are due to the fact that adaptive variations and accommodations may coöperate in dealing with conditions in a harmonious way. When variation with adaptation prepares the way for and controls innovation with accommodation, we have coincident partition and election. When innovation with accommodation prepares the way for and controls variation with adaptation, we have coincident isolation and selection.

13 *A Colony of Cats that have lost Aversion to Wading and Swimming.*

The interaction of the principles of segregation is illustrated by the Tarpon Island cats. One of the most decided instincts of the ordinary cat is to avoid immersion in water or any other liquid. His inherited nature leads him to dislike to wet even his feet; but there may arise conditions under which he will use his paws in drawing food out of the water. More than one has learned to help himself to cream placed in an open jar by thrusting his paw into the liquid and then licking off what adheres. Some have learned to skim pans of milk in a similar way, and others have become adepts in fishing for goldfish kept in glass globes or aquaria. These undoubted examples of the partial overcoming of their natural aversion renders it easier to believe the following account of a complete change of habits in a certain isolated group of cats.

According to the New Orleans Times-Democrat* there are on the shores of Louisiana, near the mouth of the Mississippi river, two types of cats. The great majority are like the cats of other regions, but a small tribe on Tarpon Island have apparently lost all aversion to being in the water. Their separation from other families of cats has allowed of their establishing their habits of feeding on entirely new lines of tradition, for they all wade freely in the shallow waters of the beach hunting for small fish; and three or four of the bolder ones swim off to oyster boats lying at anchor near by. This is an example of partition allowing an innovation to be established through election as a permanent habitude; and as Captain Bosco, who owns these cats, says it is many years since they began to go into the water, we have reason to believe that coincident selection has begun to operate in producing a breed whose innate instincts are better adapted to this mode of life than were those of the original stock from which they sprang; or may it not be possible that the direct inheritance of acquired characters has removed the instinctive aversion to water that belongs so universally to cats? If, now, after the habits and innate instincts of the new breed are well established, several pairs of them should be taken to a part of the shore where other cats possessing the usual instincts of the species are found, it is possible that their special endowments and social habits might lead them to associate with each other, and thus to perpetuate the habits already formed, and to breed with each other. If such should be the case, it would be an example of social and industrial partition, leading to discriminate isolation and tending to produce permanent segregate breeding. As, however, the segregative social instincts of the cat seem to be weak compared with those of most mammals, the opportunity for establishing separate races of cats is not as good as in the case of most domestic species.

14. *Coöperation of Structural Isolation and Structural Selection Illustrated.*

The correlation that may exist between a given form of isolation and the corresponding form of selection is seen in the case of the different forms of impregnational isolation and impregnational selection. Let us consider the case of two varieties of the same species of land snails that are prevented from crossing by the fact that in one variety the sexual organs are on the right side of the body (the male organs being near the head and the female organs a little further back), while in the other variety they are arranged in the same way on the

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* New Orleans Times-Democrat, probably January, 1900, as it was copied by a Philadelphia paper late in January, 1900.

left side of the body. The first is called a dextral variety, and bears a dextral shell. Each individual has both male and female organs, and any two dextral individuals easily unite and impregnate each other, as do also any two sinistral individuals. But if a dextral individual and a sinistral are brought together, I think it will prove impossible for them to impregnate each other owing to the lack of correlation in their forms. I earnestly hope that in the Hawaiian Islands, where there are not a few species represented by both dextral and sinistral varieties, careful investigation of this point will be made.

I anticipate that crossing between dextral and sinistral forms will be found to be impossible. If this is so, it is probable that if, in a group of one form occupying one tree, there arise in the same generation two or more individuals of the reverse form from the original stock, they will mate; and there will be formed, without intergrading steps, a completely segregated group, determined in the first place by structural isolation. It should, however, be noted that when the representatives of any species found on any one tree are all either dextral or sinistral, any single individual of the reverse form that may appear in any generation will be prevented from leaving offspring, and the result will be structural selection, a form of reflexive selection determined by and coöperating with structural isolation.

Let us now consider whether environal selection is one of the causes that produces both dextral and sinistral varieties occupying the same valley and often sharing the same groves or the same individual trees, and for the sake of definiteness let us suppose that the original form entering the valley was dextral. We then ask:

(1) Did the two or more sinistral individuals originating the new type gain any advantage from their sinistral form when they first appeared?

(2) Does the colony as it now exists derive any advantage from their form that they would not equally enjoy if they had all remained in the original dextral form?

(3) If a colony of sinistral individuals occupying a given candlenut tree and a colony of dextral individuals occupying another tree of the same species are made to exchange trees, will each group find themselves unfitted for the new position?

My observations on dextral and sinistral varieties of Hawaiian snails lead me to believe that in every case all three of these questions should be answered in the negative; and that, therefore, the formation of this distinction can not be attributed to natural selection, nor, indeed, primarily to any form of selection. After the new form has been produced by variation and preserved by structural isolation, structural selection may coöperate in maintaining the same; but the new form of selection is entirely dependent on the isolation which has opened the way and partially established the new form.

The production of a sinistral form by a dextral species, or of a dextral form by a sinistral species, is a striking example of what De Vries calls mutation.* Undoubtedly new forms have sometimes arisen in this sudden way and have been continuously propagated without the aid of man in securing artificial segregation. But that it is the exclusive or even the predominant method by which divergence of species takes place has not been shown. In the case of sinistral snails the question naturally arises whether there are certain habits of life that favor this form. Can any reason be found why this form is much more common among those groups of species that are entirely arboreal in their habits than among those that live on the ground? Does the position assumed by those that cling to the underside of branches, or to the perpendicular trunks of trees, facilitate the production of young of the sinistral form?

15. *Some Young Snails have the Reverse Coil from that of their Parents.*

Since writing the above, my attention has been called to the following statement by Dr. A. G. Mayer,† concerning certain species of Partula found on the island of Tahiti:

> The young of dextral or sinistral snails are usually dextral or sinistral respectively, but this is not invariably the case. It is interesting to observe, however, that *all* of the young developed within any given adult [at the same time] are either dextral or sinistral, never some of them dextral and others sinistral. The young are born one at a time, three eggs and two or three young snails in various stages of development being often found in a single adult animal.

This seems to indicate that the causes producing in the young a reversed coil from that in the parent operate alike on each embryo within the parent at the same time, and are likely to produce more than one individual of the reversed form when any are produced, and so to open the way for a new racial type, which we have reason to believe is completely segregated from the original type, though both occupy the same valley, or even the same tree.

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* An interesting article on "The Origin of Species," by De Vries, translated from "Album der Nature," and revised by the author, will be found in the Popular Science Monthly for April, 1903. See also an article by the same author in Harper's Magazine for January, 1905.

† Memoirs of the Museum of Comparative Zoölogy at Harvard College, Vol. XXVI, No. 2, pp. 121, 122.

16. *Mutations and Varieties.*

In a recent volume by Prof. T. H. Morgan (Evolution and Adaptation, 1903) we find an interesting exposition of the mutation theory, from which we quote a few sentences:

> Amongst the mammalia and birds of North America there are many cases of local forms or races, some of which at least are probably mutations. This can only be proven, however, by actually transferring the forms to new localities in order to find out if they retain their original characters or become changed into another form [p. 292]. As De Vries has pointed out, each mutation may be different from the parent form in only a slight degree for each point, although all the points may be different. The most unique feature of these mutations is the constancy with which the new form is inherited. * * * There is another point of great interest in this connection. Many of the groups that Darwin recognized as varieties correspond to the elementary species of De Vries. These varieties, Darwin thought, are the first stages in the formation of species, and, in fact, can not be separated from species in most cases. The main difference between the selection theory and the mutation theory is that the one supposes these varieties to arise through selection of individual variations, the other supposes that they have arisen spontaneously and at once from the original form. The development of these varieties into new species is again supposed, on the Darwinian theory, to be the result of further selection; on the mutation theory, the result of the appearance of new mutations. * * * Some of the advantages of the mutation theory may be briefly mentioned here.
>
> 1. Since the mutations appear fully formed from the beginning, there is no difficulty in accounting for the incipient stages in the development of an organ, and since the organ may persist, even when it has no value to the race, it may become further developed by later mutations. and may come to have finally an important relation to the life of the individual.
>
> 2. The new mutations may appear in large numbers, * * * and the danger of becoming swamped through crossing with the original form will be lessened in proportion to the number of new individuals that arise.
>
> 3. If the time of reaching maturity in the new form is different from that in the parent form, then the new species will be kept from crossing with the parent form, and since this new character will be present from the beginning, the new form will have much better chances of surviving than if a difference in time of reaching maturity had to be gradually acquired.
>
> 4. The new species may be in some cases already adapted to live in a different environment. * * * and so will be isolated from the beginning. * * *
>
> 5. It is well known that the difference between related species consists largely in differences of unimportant organs, and this is in harmony with the mutation theory, but one of the real difficulties of the selection theory.
>
> 6. Useless or even slightly injurious characters may appear as mutations, and if they do not seriously affect the perpetuation of the race, they may persist (pp. 297–299).

17. *Theories Compared.*

It will be observed that in the above-quoted statements recognition is given to the following facts, to which attention was called in the papers reproduced in the Appendix of the present volume.

(1) That there may be divergent varieties that are not produced by exposure to different environments.

(2) That these varieties are often local.

(3) That when isolated the peculiar character of the variety is not swamped by crossing.

(4) That these varieties may be so accumulated as to produce divergent species, whose differences are not due to differences in the environment.

(5) That the differences found in allied varieties and species are often differences that are not necessary for the survival of the different groups.

This series of important facts that have been either overlooked or assumed to be impossible by a leading school of evolutionists are, I believe, fully recognized by the expounders of the mutation theory, though it seems to me that a fuller explanation may be given than any they have offered. It seems to me that both the Darwinian theory and the mutation theory are lacking in that they have not given sufficient attention to the influence of isolation, first in protecting divergent types, whether great or small, second in cutting off all community of action in the different forms of reflexive selection, and third in opening the way for diversity of environal selection, through diversity in the methods of dealing with the environment. They have also failed of recognizing that this controlling influence, arising from methods of using the environment, and leading to increasing divergence in succeeding generations, may find its starting point in the individual peculiarities of the founders of the colony, whether these peculiarities be inherited aptitudes or acquired habitudes. The Darwinian theory is deficient in that it has no explanation of the divergent evolution of two isolated groups of the same species exposed to the same environment. The mutation theory recognizes that the individuals starting one colony may happen to be of a different mutation from those forming the other colony, and that, therefore, the colonies may be different from the first generation; but it fails to give any explanation of why they should become increasingly divergent in the generations that follow. In opposition to the Darwinian theory, it denies that any permanent effect can be produced by the selection of individual variations, and, therefore, if two pairs of individuals belonging to the same mutation should become the parents of two isolated colonies, it ought to predict that every variation occurring in either colony will be found in both, and in the same proportion. That this will be the case has not yet been shown.

Without variation in its different forms coöperating with heredity, isolation and selection could have no influence in guiding and shaping evolution. It is, therefore, well that the mutation theory insists on the importance of these fundamental factors and of the laws by which they are controlled. But it must be remembered that through the powers of variation and heredity the principles of free crossing, isolation, and selection gain profound significance. These latter are the conditions through which the laws of the fundamental factors are revealed; and if we misinterpret the laws we shall fail in our explanation of the process. These laws have not been fully brought to light; but is there no reason to suspect that there is something lacking in the theory that the selection of individual variations can have no effect on the final result? *

18. *Degeneration of Species when the Standard of Survival is Lowered.*

The frequently observed fact that characters built up by the artificial selection of individual variations gradually disappear when the selection entirely ceases seems to be the chief reason for disregarding the influence of such variations in the formation of varieties and species. But is not the same tendency seen in the characters of natural species which the mutation theory assumes to have resulted from mutations? Are there not characters that have been maintained with unbroken constancy through countless generations of ancestors, not only through all the past history of the present species, but through the much longer history of many ancestral species, and that yet do not reach, in every individual of the species, the standard necessary for survival? If such individuals are able to escape the fate that has overtaken similarly defective ones of previous generations they will help to lower the standard of attainment previously gained by the species to which they belong. This process may be repeated in successive generations till the character is entirely lost. Different stages of such a process are revealed in the present condition of certain species of birds, in regard to the instinct that leads the mother bird to sit on the eggs she lays, and to provide for the young when

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* Prof. T. H. Morgan's position is seen in the following statement: "Nature's supreme test is survival. She makes new forms to bring them to this test through mutation, and does not remodel old forms through a process of individual selection." See "Evolution and Adaptation," p. 464.

they appear. The American cowbird and the English cuckoo seem to have entirely lost the instinct. Again, the physiological power of the mammalian mother to provide milk for her young seems to be gradually declining in the human species, through the survival and propagation of the children of mothers presenting individual variations below the standard that for countless generations was necessary in order to leave descendants. If statistical investigation should show that lack of sufficient milk for their young is most common in mothers belonging to communities that have for the longest time, and most successfully, met every deficiency of this kind, it would be a strong indication that the accumulation of individual variations can not be overlooked in a complete theory of the factors of evolution.

19. *Degeneration in Eyesight and its Lessons.*

Another example of a similar kind is found in the power of sight in mankind. I believe it is fully recognized that in civilized races the proportion of individuals with defective sight is much greater than in savage races; and the best explanation that has been given is found in the equally certain fact that with civilized man the standard of sight necessary for individual survival has been reduced to zero, and the standard necessary for attaining the highest prosperity and the fullest share in the propagation of the race is far below that which is necessary among savages. Is there any reason to doubt that the difference in the average inherited power of vision in the two cases is due to the fact that for many generations individual savages with deficient sight have had less opportunity for leaving descendants than have individuals with the same deficiency belonging to civilized races? Without the selection of individual variations in the primitive races of man, the power of these races would have fallen so low that the species would have been exterminated in its conflict with other species. But the survival of man, due to this selection of individual variations, is in no small degree determining what other species shall survive; and the determination of the species that survive controls the types of the mutations that from time to time appear, and would, therefore, control the types of future species, even if every such new form must find its origin in a mutation.

First Lesson.—It therefore seems to be shown that the accumulation of individual variations by selective generation has had, and must continue to have, a profound influence on the course of evolution; for, if the selection of individual variations has significance in the *survival* of species in one period, it must have significance in the *origin* of species in the periods that follow. The sinistral mutations produced by the Helix are different from those produced by the Achatinella. The short-legged lamb, from which sprang the Ancon sheep, was not the suckling of a lioness, but had a sheep for its dam. In other words, the segregations and survivals of one generation control the types of heredity and variation (including mutation) in the next generation.

Second Lesson.—If the selection of individual variations is necessary for the maintenance of the normal standard of eyesight in the human species, is it not possible that the same necessity exists in other species? And may it not be true that many other inherited endowments are subject to gradual decay when the standard of selection is lowered? If we find, in a given country, that the mothers who have to feed their babes on artificial substitutes for mother's milk lose a larger per cent of their children than do those who are able to give suck, does it necessarily follow that the power of giving suck is increasing from generation to generation among the people of that country? In the language of the statistical method, is it not possible that the "skewness" of the "frequency curve" (for different grades in the power of furnishing milk) might, in such a case, give some indication of the selection that is taking place, and that, at the same time, the statistics of successive generations might show that there was no gain in the power? Or, in such a case, would there be no skewness in the frequency curve, though there is constant selection that results in the maintenance of a constant standard?

20. *Degeneration in Breeding Instincts.*

In the case of the Old World cuckoo it may be a question whether the loss of the maternal instinct (or rather of this series of instincts), came in a single generation, by one mutation, maintaining its type with constancy from the first; or by several successive mutations, each mutation being added to the previous ones, and being persistently inherited; or whether the process has been a very gradual accumulation of individual tendencies through the success of aberrant individuals in leaving descent, and so lowering the general standard of service for the whole species. There are, however, certain facts that point toward the last of these as the process by which the degeneration has taken place. F. M. Chapman, in his Handbook of Birds of Eastern North America, notes that "Many species [of cuckoo] are remarkable for the irregularity of their breeding habits." Of the Ani, a genus of the same family, he says: "The Anis are communistic, and build but one nest, in which several females lay and share the task of incubation." Now, it is manifest that, in a community of this kind, one mother-bird might fail of doing her share of the task of incubation or of feeding the young, and still be represented by descendants, a result that would, in the next generation, slightly lower the average standard in the instincts that secure faithful service. Man may perhaps be able to devise more than one method of forestalling the degeneracy that tends to arise from communal methods of providing for the young; but for the simple-minded Ani there would seem to be no possible way by which it may prevent the slowly increasing decay of parental instincts. The probability is that in the course of a few hundred generations the coöperative method of incubation and of providing for the young will break down through the general tendency to shirk the task; and the more degenerate members, who have heretofore imposed on their own kindred, will find it equally easy to lay their eggs in the nests of other species and so establish the method that has already been reached by at least two species.

I am informed by Prof. Lynds Jones of an irregularity in the habit of two species of American cuckoos which may throw some light on the possible steps by which the greater degeneracy of the Old World cuckoo has been reached. The yellow-billed cuckoo and the black-billed cuckoo are clearly marked species, both found nesting in Eastern North America. Usually a nest of either species contains only the eggs or young of that species, but occasionally an interloper of the other species is found. If a delinquent individual of either of these species sometimes lays an egg in the nest of another species, is it not probable that it has failed to build any nest of its own and is leaving all its eggs for the season to the care of other birds, usually laying them in the nests of birds of the same species and thus escaping the inquisitive impertinence of the ornithologist, who finds the eggs all of one color, and passes without suspicion? At any rate, the faithful workers of the species seem to have no method of dealing with the delinquents or of preventing the blending of their descendants with the descendants of the faithful. There is, therefore, some reason to fear that these two species have entered on a path that will lead to extinction, unless, like the Old World cuckoo, they succeed in shifting the work of raising their young ones on to other species of more sturdy instincts.

Whether the change in the Old World cuckoo came by sudden mutation or by gradual accumulation of individual variations, it was certainly a regressive process, undoing instincts that had been inherited for countless generations.

21. *Mutation as recently expounded by De Vries.*

As "Species and Varieties, Their Origin by Mutation," by De Vries, 1905, has appeared while the present volume is being put into type, I add a few words on the very interesting experiments there described. In his first lecture he fully endorses Morgan's interpretation of the mutation theory and speaks of the lectures that are to follow as "a review of the facts obtained from plants which go to prove the assertion that species and varieties have originated by mutation, and are, at present, not known to originate in any other way." (See p. 9.) The experiments described in Lecture XIX show that Lamarck's evening primrose, as it now exists in Holland, is subject to mutation; for over two per cent of the seed taken without selection from plants that have been grown without crossing and in rich soil for two or three generations, produce clearly marked digressions from the original stock. About half of these mutations produce the variety with oblong leaves, while the remaining half produce several other types. (See p. 556.) In all, twelve new types have been observed, of which nine are entirely constant as long as they are kept isolated, and three, though kept unmixed, produce both the original type of the species and the new type. His record indicates that selection has not been used in producing these results; but how different are the facts given in the production of the double-flower variety of the corn-marigold. His description indicates that careful selection, during successive generations, of seed from flowers furnishing the largest number of ray-florets brought the average number of these rays up to 21 in the third generation, to 34 in the sixth, to 47 in the eighth, and to 55 in the ninth generation. In the seventh generation three heads were produced with a few rays in the midst of the disk; in the eighth generation the maximum number of rays (counting both internal and external ones) was 100, in the ninth generation 200. "All the children of this original mutated plant [the plant producing the three heads just mentioned] showed the new character. * * * Not on all the heads, not even on the majority of the heads on some individuals, but on some heads all gave clear proof of the possession of the new attribute." (See p. 504.) My only suggestion is that since the selection of fluctuating variations for six generations was necessary in order to reach the new character which is called a mutation, and for three more generations in order to perfect the type, selection should be regarded as a part of the process producing the new type. On pages 468–478 he describes another experiment with another species, commencing with successive selections of fluctuating variations and culminating in a mutation that becomes stable.

22. *Selection and the Inheritance of Acquired Characters.*

The inheritance of functional variation, if proved in any case, does not prove that selection has had no influence in shaping the characters of the same species. In a recent volume by J. T. Cunningham, entitled "Sexual Dimorphism," a large collection of very interesting facts on the subject of secondary sexual characters has been presented. It, however, seems to me that but little proof has been given of his contention that these characters have been produced, not by selection, but by the action of direct stimulation on the individual, facilitated and strengthened in successive generations by an increasing inheritance of the effects of stimulus in previous generations. Whether acquired (*i. e.*, functional) characters and tendencies can be inherited demands most careful investigation; but if it is found to be a fact it will not disprove the importance of the different forms of selection in determining the special kinds of response that the function awakens. Hertwig is undoubtedly right when he says that neither selection nor the inheritance of functional variations determines whether a given bee's egg shall develop into a drone, a queen, or a worker, for the determining influence is the power of responding in different ways to different conditions. The question, however, remains as to why the workers of the Italian bee develop in such a way as to produce a long tongue, while certain other bees develop a comparatively short tongue. Hertwig admits that selection has had much to do with this diversity in the powers of response.

In Prof. C. B. Davenport's two volumes on "Experimental Morphology," a large mass of facts illustrating the different responses of organisms to external conditions has been brought together, and in certain cases the effects are found to increase in successive generations when there is reason to believe that the increase is not due to selection. Though the inheritance of acquired characters may be proved by these experiments, I judge that Professor Davenport does not doubt that the different forms of selection have an important influence in shaping the specific characters of the same organisms.

CHAPTER VI.

ANALYSIS OF THE FOUR PRINCIPLES OF SEGREGATION, WITH ILLUSTRATIONS.

I. Chief Divisions of the Four Principles.

1. *Six Conditions on which the Racial Evolution of a Cross-Fertilizing Group must rest.*

Before we proceed further with the analysis of the principles producing segregation, we shall enumerate certain vital conditions which must be constantly present in order that there should be any divergent evolution in allogamic (*i. e.*, cross-fertilizing) organisms. Besides individual assimilation and growth there must be, first, the power of reproduction; second, survival (that is, the number and adaptations of individuals produced by members of the group must be sufficient to meet the losses through death in the struggle for life), for otherwise the group will be exterminated; third, variation (that is, tentative diversity in individual innate characters and aptitudes); fourth, heredity (that is, the reproduction of fundamental racial characters), and, therefore, the continuance of types; fifth, free crossing between the males and females of the different variations of any one group; sixth, segregate intergeneration (that is, the breeding of like with like), setting limits to the sphere of free crossing, and so controlling variation and heredity.*

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* It will be observed that I regard heredity as one of the fundamental powers on which the evolution of organisms depends. If there were no heredity a protozoa might, in one generation, produce the highest as well as the lowest types of organic life; an elephant might be the father of a mouse, and a cabbage might be the mother of a rational child. The importance of variation in the process of evolution can not be overstated; but there can be no variation except as there is a type from which the variation departs, and heredity is the maintenance with more or less exactness of the ancestral type. This being so, it seems impossible to accept Prof. H. S. William's theory that "Variation, and not heredity, is the fundamental characteristic of the phenomena of organisms." (See article on "Variation *versus* Heredity," American Naturalist for 1898, p. 831.) In this case, as in many others, the propositions that we may rightly make concerning a principle depend on our definition of the principle. If heredity is defined as absence of the power to vary, Prof. Williams's contention may be justified. If, on the other hand, we define it as the power to maintain a type in the midst of variation, we must regard it as one of the fundamental characteristics of the organic world.

These six conditions all relate to reproduction. The first and second are that there must be reproduction, and that it must be sufficient with the aid of adaptation to perpetuate the race. The third and fourth are that the reproduction must result in individuals more or less departing from the average character of the parents, but corresponding with them in their fundamental character. The fifth is that reproduction involves the coöperation of separate individuals and binds the intergenerating group together in a common heredity. The sixth is that divergence of character depends on the prevention of free intergeneration, loosening the bond of common descent between the isolated sections, and so opening the way for the divergent forms that variation and heredity controlled by segregation are permitted to produce. The causes preventing free intergeneration, and opening the way for divergence, may lie in the organism or be imposed from without.

2 *Six Conditions on which the Evolution of Habitudinal Types must rest.*

First, the power of influencing associates; second, success (that is, the number of the socially endowed individuals must be sufficient to keep up the organization); third, innovation (that is, tentative diversity in the action of individuals in invention and initiation by means of experiment, comparison, and repetition of the best); fourth, tradition (that is, influence by means of example and imitation); fifth, free association and communication within the social group; sixth, segregate association setting limits to the sphere of free association and so controlling innovation and tradition.

3. *The Modes of the Four Principles.*

In the classification which I have found most convenient, each of the four principles of segregation is presented under two main forms or modes, besides a third covering the reverse or regressive aspects. I also recognize that the indiscriminate action of any one of the four principles may produce results that should not be overlooked. The indiscriminate principle sometimes producing racial intensification is indiscriminate elimination of all but a few, and the indiscriminate principle sometimes producing habitudinal intensification is indiscriminate failure of all but a few. Under selection we have first the two modes, *j*, reflexive selection, determined by the direct influence of members of the species upon each other, as in sexual selection and social selection, and *k*, environal selection, determined by the relations between the environment and the species. But each of these modes may be presented in its regressive aspects under *l*, regressive selection, due to the survival of variations previously excluded; and in its indiscriminate aspects under *z*, indiscriminate elimination. So also election, and isolation, and partition has each its reflexive mode, produced by the action of the members of the species upon each other, and its environal mode, determined by the relations between the environment and the species; also its regressive aspects, caused by the cessation or reversal of the influence that has been ruling, and its indiscriminate aspects. The letters (*j*, *k*, *l*, *z*) here used in designating the different forms correspond with those used in the tables given in Chapter VIII.

4. *The Reflexive Mode of Influence.*

The forms of *reflexive selection* have been more fully worked out than have those of *reflexive isolation*, or *reflexive election*, or *reflexive partition*. Of the forms of reflexive selection, sexual selection is the most familiar; for Darwin discussed its effects on the evolution of the higher animals and especially emphasized its importance in producing the different races of man. It may be found that some of the effects which he attributed to this principle are produced in other ways; but there can be no doubt that in the evolution of mankind it is a factor of the greatest importance. With the advance of civilization the action of natural selection is checked; but the result is not as disastrous as it otherwise would be but for the increasing stringency of sexual, social, and institutional selection in preventing the marriage of those who are most deficient. Darwin recognized that the forms of sexual selection may not only change without any change in the environment surrounding the species, and without securing any advantage for the species in its relations to the environment, but that it may even establish a standard of selection that is somewhat at variance with the standard maintained by natural selection, and that it may in such cases be the deciding influence, causing the species to lose certain characters which are at the time of the change of some advantage in its relations to the environment. This he thought must have been the case when the ancestors of the human race first lost their covering of hair. (See Descent of Man, Chap. XX.) The emphasis that Darwin laid on the action of sexual selection in securing the coördination between the sexual instincts of either sex and the instincts and palpable qualities of the other sex has gradually led to the recognition of certain other coördinations between members of the same race, which must be secured by other forms of reflexive selection. These other forms are like sexual selection, in that they are subject to change without change in the environment of the species.

II. Methods of the Reflexive Mode of each of the Four Principles.

Producing demarcation of habitudinal groups:
- *Reflexive partition.*
    - Conjunctional partition.
    - Institutional partition.

Producing intensified divergence in habits of groups:
- *Reflexive election.*
    - Conjunctional election.
    - Dominational election.
    - Institutional election.

Producing demarcation of racial groups:
- *Reflexive isolation.*
    - Conjunctional isolation.
    - Impregnational isolation.
    - Institutional isolation.

Producing intensified divergence in racial characters:
- *Reflexive selection.*
    - Conjunctional selection.
    - Dominational selection.
    - Impregnational selection.
    - Institutional selection.
    - Prudential selection.

These adjectives designate the methods of action by which the members of an associating and intergenerating group influence each other in such a way that the attainment of certain standards of training and of inheritance are necessary to gain a full share in shaping the habits of the group and in propagating the species. But if partition and isolation divide the original group into two or more associating and intergenerating groups, the way is opened for divergence between the separate groups; for the standards gained by reflexive selection and reflexive election are all subject to gradual divergence through the fact that different standards of size, weight, etc., may bring survival and success to the separate groups in which these differences are found. For example, the bantam fowl, which for many generations has been isolated from the other breeds of barnyard fowls, lays an egg smaller than that of the Shanghai fowl; but the coördination between the average size of the egg and the average size of the breed of fowls laying the egg is equally attained in each case by filio-parental selection, which is one of the forms of conjunctional selection.

In our investigation of the different methods of influence resulting in segregation, it will greatly facilitate our comprehension of the subject if we first consider how a given method of influence determines certain forms of selection; then how far the same method of influence shapes the forms of election determining the acquired characters of the group; then what its isolating effects may be; and finally how the same method of influence may divide an original group of freely associating individuals into several smaller groups and so produce partition. Having mentioned the chief methods of the reflexive influences aiding in the demarcation and intensification of habitudinal and racial groups, it will next be in place to consider the way in which each method of influence acts and the different forms of action that it assumes in producing results under each principle.

1. *The Forms of the Conjunctional Method of each of the Four Principles.*

Producing demarcation of habitudinal groups:
- *Conjunctional partition.*
  - Family partition.
  - Social partition.

Producing intensified divergence in habits of groups:
- *Conjunctional election.*
  - Sexual election.
  - Social election.
  - Filio-parental election.

Producing demarcation of racial groups:
- *Conjunctional isolation.*
  - Sexual isolation.
  - Social isolation.

Producing intensified divergence in racial characters:
- *Conjunctional selection.*
  - Sexual selection.
  - Social selection.
  - Filio-parental selection.

The conjunctional method of influence is due to the need of coördination between one sex and the other in the intergenerating group, between each member and the others in an associating group, and between the parents and offspring in each family group.

2. *The Sexual Form of Selection, Election, and Isolation.*

Sexual selection is due to the necessity for coördination between the sexual instincts and palpable qualities of the individual of either sex and the instincts and palpable qualities of the other sex, in order to secure propagation with survival in subsequent generations. It is often assumed that in creatures lower than man sexual selection may be effective in establishing the normal standards of prowess and display in the male sex, but that it avails very little in determining the standards of attainment in the female sex. This is in a considerable degree true of species in which the male is the party that seeks and calls for a mate; but even in these species the answering call of the female is often a necessary feature in the attainment of suitable mating; and the hen-bird that has lost her voice goes desolate. In some species of insects the call for a mate comes from the male, and the part of the female is to respond by leaving its distant hiding-place and coming to the male. The methods of one such species are described in my paper on Intensive Segregation, reproduced in Appendix II of this volume.

Sexual election is due to the necessity for coördination between the acquired habits and standards of the individual of either sex and the sexual instincts, as well as the acquired habits and standards of the other sex, in order that the individual may secure success and influence in the community.

William E. D. Scott, curator of ornithology of Princeton University, tells of a red-winged blackbird which, for the sake of testing the power of tradition, was, from the day he left the egg, "brought up by hand, in a room by himself, away from all sounds, as was supposed. The result was that when the time came for him to sing he crowed like a rooster. It then developed that every morning a bantam rooster had crowed under his window."* Whether he was able to win any mate among his fellow captives is not mentioned; but if he had been turned loose to seek a mate among his kindred of the wild, his inability to use the song of his kind would certainly have given great advantage to his rivals who had learned the true song of the species.

Sexual isolation arises between groups of the same species that have been separated by geographical barriers for several generations, and have in the meantime attained divergent forms of inherited characters by which they recognize each other, and different methods of calling each other and winning each other. Though physiologically any cross between the two races is both fertile and vigorous, psychologically they are prevented from crossing through incompatibility in sexual instincts and inherited endowments.

I judge that there is no need of distinguishing sexual partition from sexual isolation, for an associating group determined by sexual habits and instincts would surely be an intergenerating group.

3. *The Social Form of Selection, Election, Isolation, and Partition.*

Social selection is due to the necessity for coördination between the social instincts and endowments of the individual and the social instincts and endowments of the race, in order that the individual should secure a chance to survive and propagate. We find that under the same environment there are many possible instinctive calls, and many arrangements of color, and many combinations of inherited odors, by which the individuals of one race recognize each other. By means of characters that we are unable to note the bees of one hive recognize each other, and there is reason to believe that serious deficiency in any essential character would lead to the exclusion of the deficient individual from the privileges of the community. The power to recognize one's own race by scent is not as wonderful as the power of the bloodhound to distinguish between individuals in the same way. Not only must the distinctive character of the race be

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* See The Outlook (of New York) for July 5, 1902.

found in the individual, but the individual must be able to recognize those of his own clan, and to keep with them in time of rapid flight. A near-sighted deer or cotton-tail rabbit would be in danger of losing his life through losing the trail which the leaders have taken, raising their tails high that they may be seen by those which follow.

Social election is a similar principle resting on *acquired habits and characters.* It is due to the necessity for coördination between the social habits of the individual and the social standards of the community, in order to secure success and influence. The knowledge of a common language is recognized as a fundamental need of a human community, and there is a similar need in any community of animals. With the lower creatures this need is largely met by inherited instincts, which determine the calls and warning cries and the interpretations that they receive; but in some cases the training obtained by the young from the example of their elders is an important element in the transmission of the language. In such cases the standard is maintained by social election.

It is easy to understand that the red-winged blackbird mentioned above, which learned to crow, but had no chance to learn the normal song of the species, would not have much influence on the musical attainments of the next generation of the species; and perhaps his failure in this respect would lessen his influence as a leader in other things.

One reason for believing that example has no small influence in shaping the songs of certain species of birds, is found in the fact that Japanese, who highly appreciate the song of the uguisu (sometimes called an oriole), are very careful that the young birds that are taken from the nests of wild birds in the woods and brought up by hand shall have opportunity to hear only the most accomplished adult singers during their period of growth.

Social isolation.—When two groups of a species have been separated by geographical barriers for many generations, they are liable to gain divergent social habits and instincts, and different calls, rendering them unfit for being associated in the same intergenerating group when brought into the same district. The geographical isolation has ceased, but they continue as separate intergenerating groups through the influence of social isolation.

Social partition.—In so far as the social incompatibilities holding two groups apart are due to acquired habits and tend to produce separately associating habitudinal groups, the process may be called social partition.

4. *The Filio-parental Form of Selection and Election, and Family Partition.*

Filio-parental selection is due to the dependence of survival on the coördination between the inherited needs, powers, and instincts of the young by which they are related to their parents and the inherited adaptations, powers, and instincts of the parents by which they are related to the young. In my paper on Intensive Segregation I referred to the necessity for coördination between the size of the child's head and the size of the pelvis in the mother.

In Science for December 24, 1897, page 942, G. A. Reid, of Southsea, England, calls attention to the increasing difficulty of childbirth in civilized women, resulting from the regressive selection occasioned by the skillful appliances of modern science. He says: "Indeed the recent advance of obstetric science has enabled so many of the otherwise unfit to survive among us for some generations past that now numerous women are quite incapable of parturition without instrumental aid." In a note he adds: "It is not possible that the saving of so many narrow-hipped women and big-headed children can have left the race unaffected."

Filio-parental election is due to the necessity for coördination between the acquired habits of the young and the habits, instincts, and endowments of the parents in order to gain success and influence.

The term "family isolation" may be needed in describing the usual relationship of mates in certain species; but with mammals it has been found that in-and-in breeding, continued through many generations, tends to degeneration, and, therefore, to extinction.

Family partition arises in so far as the separation of families leads to the formation of separate habits and acquired characters. It is doubtful whether the term "filio-parental partition" is needed, as the term "family partition" seems to be more appropriate.

5. *The Forms of the Dominational Method of Influence.*

- Producing intensified divergence in the habits of groups:
  - *Dominational election.*
- Producing intensification of racial groups:
  - *Dominational selection.*
    - Sustentational domination.
    - Protectional domination.
    - Nidificational domination.
    - Mating domination.
    - Prepotential domination.

The dominational method of influence does not depend on superior adjustments to the environment, but is due to the power to outdo, overcome, and forestall rivals of the same species in taking possession of mates or of resources and in seizing on opportunities. The importance of conflict and rivalry between individuals of the same group in gaining possession of resources and mates was discussed in my paper on Intensive Segregation under the term that I now use. It has since then been discussed by Karl Pearson in his "Grammar of Science," under the term "inter-group selection." The chief objection to his term is that it ought naturally to include all the forms of what I have called "reflexive selection;" but this is not in accordance with the definitions he has given.

Dominational selection is due to inherited powers for overcoming rivals giving a larger share in propagation and survival through control of resources and mates.

Dominational election is due to acquired powers for overcoming rivals giving superior success and influence in the associating group. As prepotence is determined entirely by inherited powers, dominational election can have no influence on prepotence. Severe competition with domination is a condition that gives importance to isolation and partition, but these principles are not introduced without other causes, such as migration or transportation.

6. *The Forms of the Impregnational Method of Influence.*

Producing demarcation of racial groups:	Producing intensification of racial groups:
Impregnational isolation.	*Impregnational selection.*
Dimensional isolation.	Dimensional interselection.
Structural isolation.	Structural interselection.
Potential isolation.	Potential selection.
Segregate fecundity.	Fecundal selection.
Segregate vigor.	
Segregate adaptation.	
Segregate freedom from competition.	
Segregate escape from enemies.	

The impregnational method of influence is due to the need of coördination between the size, structure, sexual elements, and functions of each sex and the related characters of the other sex, in any intergenerating group, in order to secure a sufficient number of impregnated germs with the least expenditure and waste. Inasmuch as the influences shaping impregnation are inherited and not acquired, their chief effects are on racial rather than habitudinal groups. We therefore have no occasion to consider impregnational partition and election.

Of the forms of impregnational isolation, the first five as given above were so fully considered in my paper on Divergent Evolution* that it

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* See Appendix I, where part of the paper is reproduced.

will not be necessary to give much space to them here. Of the forms of impregnational selection, the last of the four mentioned above was presented in my paper on Intensive Segregation* as a factor of profound influence in the intensification of racial groups. The term there used is "fecundal intension" which indicated the result of the process which I call "fecundal selection."

7. *The Dimensional Form of Impregnational Selection, and of Isolation.*

The dimensional form of impregnational selection is due to the necessity for the coördination of the sexes of the intergenerating group, in such a way that incompatibility of size shall not interfere with impregnation. Compatibility in this respect is maintained within the intergenerating group; for if any individual is so far above or below the average size as to render mating difficult, the chances are that the descendants of that individual will be comparatively few, or perhaps entirely wanting. This may be called dimensional interselection.

Dimensional isolation arises when local varieties of birds and mammals, that have become very divergent in size, are brought to the same district. An example is seen in bantams and Shanghai fowls. There are also certain breeds of horses and of asses that are completely prevented from crossing with certain other breeds of the same species, through incompatibility in size. Dimensional and structural isolation are terms that convey a fairly definite meaning, as it is evident that the isolation must be brought about by the relations of members of the same species to each other, and not through their relations to the environment surrounding the species. There would, however, be indefiniteness in the terms "dimensional" and "structural" selection; for size and structure have survival value in the relations of the members of the species to the environment, as well as in their relations to each other. I therefore prefer to call the former of these factors the dimensional form of impregnational selection and the latter the structural form of impregnational selection. If briefer terms are desired, it will perhaps be allowable to use the forms "dimensional interselection" and "structural interselection."

8. *The Structural Form of Impregnational Selection, and Isolation.*

Structural interselection.—The males of many species, especially among insects, are furnished with clasping organs for holding the females during mating, and in some cases both sexes are thus equipped. The structural form of impregnational selection maintains the average characters that are necessary for the coördination of these and all other sexual organs and of all organs that are necessary for the suc-

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* See Appendix II.

cessive steps by which impregnation is reached. This last clause is added, for we observe that in the language of recent botanists the stamens and pistils of plants are not sexual organs; and "pollen grains are asexual spores."* This, however, does not change the fact that in order to secure fertilization the pollen grain, after reaching the stigma, must be able to send out a pollen tube long enough and penetrating enough to descend through the length of the pistil to the center of the ovule, through the nucellus and embryo-sac. The coördinations required for securing these and many other steps in the process of fecundation are maintained by impregnational selection, and so far as they depend on the form and structure of organs we may call the process "structural interselection." The propagation of every sexually reproducing plant and animal must depend on such coördinations.

Structural isolation arises when local varieties that have become so far divergent in structure as to be incompatible are brought together in the same district. Darwin suggested that difference in the length of the pollen tubes and the pistils may be the cause preventing crosses between certain species of plants.

9. *The Potential Form of Selection and Isolation.*

Potential selection.—There are characters more fundamental than form and structure that must be coördinated in order to secure the fertilization of the ova that produce the next generation. The pollen of one species of plants is usually either partially or entirely ineffective if it falls upon the stigma of another species, even though both species are of the same genus. There are also certain species having two kinds of stamens producing two kinds of pollen; and the pollen from the short stamens is said to be most effective upon the stigmas of the short styles, and the pollen from the long stamens most effective upon the stigmas of the long styles. As each flower produces either a long style and short stamens or a short style and long stamens, the discriminate prepotence just described insures cross-fertilization.† But our present interest is in the fact that in pollen grains there are characters of an obscure nature which are of great importance in insuring the required potency. There is reason to believe that in every species depending on sexual reproduction there must be more or less *potential selection*, by which the coördination of the sexual elements enabling them to coalesce is maintained.

Potential isolation occurs in the two forms, *prepotential isolation* and *complete potential isolation.* Complete potential isolation exists

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* See Plant Structures, by John M. Coulter; Appleton & Co., 1900; pp. 176, 177.

† See Plant Relations, by John M. Coulter, pp. 129, 130.

between types when their sexual elements are incapable of uniting in fertilized germs under any conditions. Prepotential isolation exists when cross-fertilization is possible if the alien fertilizing element has the advantage of being applied some time in advance; but if the fertilizing element of the same variety or species is applied at the same time, or in some cases at any time during several hours that follow, mixed fertilization is prevented by the prepotence of the pure fertilizing element.

10. *Fecundal Selection.*

Fecundal selection secures coördination between the number of ova and the supply of fertilizing elements required for the fertilizing of the same in connection with methods used to secure the bringing of these elements to the ova. The coördination between the number of fertilized ova and the power of the parents or community for production, rearing, and training of offspring is secured by what I call filio-parental selection. The combined action of these two principles tends to bring the standard of fertility for the group up to the highest point that is permitted by the average capacity of the parents for producing, rearing, and training the offspring. In my paper on Divergent Evolution, read before the Linnean Society in 1887, after referring to the principles of segregate fecundity and segregate vigor, I made the following statement concerning "The Nature of *Cumulative Fertility*":

> * * * 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 the vigor and adaptation of successive generations, * * * 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.* (See Jour. Linnean Society, Zoölogy, vol. XX, pp. 247, 248.)

In my paper on Intensive Segregation, published in 1889, I discussed this principle under the term "fecundal intension," which I still retain to designate the influence of the principle in transforming races and species, which was the point of view chiefly considered in that paper. I there called attention to the fact that if in an isolated portion of a species the type of variation that attains the highest fertility is not the same as in the body of the original species, the average form of the isolated group will in a few generations become different from the average form in the original stock, even though the environment surrounding each is the same. I also noted that "the chief check to this law of *cumulative fertility* is found in the antagonistic (that is, rival, and sometimes severely competing) law of *cumulative adaptation* through adaptational selection." [See Appendix II, sec. I, 8, (15).]

I also referred to the coöperation of the two factors in the following words:

> The combined action of these two laws results in the triumphant development of the most fertile of the best fitted or the best fitted of the most fertile. Another result from their combined action is that in species well adjusted to the environment the typical, that is, the average, form of the species is not only the best adapted, but it is the most fertile; and this correlation between fertility and adaptation in the average form of the species or race is a strongly conservative principle, tending to prevent the over-rapid transformation of the race or species.

In the more exact definition of fecundal selection given above I point out that the chief condition restraining the action of this principle is found in the average power of parents for parental nourishing and postnatal rearing and training of offspring. The *initial fertility* depends on the abundance of the ova and the proportionate correlation between the numbers of the ova and the fertilizing cells; while the *final fertility* must depend, not only on these correlations producing initial fertility, but on that form of filio-parental selection which secures the correlation between initial fertility and the power of the parents to nourish and develop the ova after fertilization and to rear and train the young till they are capable of independent life. If the degree of initial fertility overtaxes the power for producing or rearing offspring, the final fertility may fall far *below* the need for survival, while if the young could only reach maturity in good condition the fertility would be far *above* the need.

Certain domestic breeds show clearly the nature of the disaster that would come to any species under natural conditions if filio-parental selection were so far suspended as to break down the coördination between the initial fertility and the power of the parents to bring the young to maturity. The Leghorn hen lays from 150 to 200 eggs in a year, and seldom cares to set. It is evident that such a race would run great risk of extinction if separated from the care of those who are in the habit of providing methods for the hatching and rearing of the young. Even if some of the race should regain the instincts required for hatching out and rearing their young, how impossible would be the task of hatching and raising twelve or thirteen full broods in a year.

Having suspended laying eggs for a few days, the hen might devote herself faithfully to setting on a nest full of eggs needing warmth for hatching; but before the chicks were ready to appear, the necessity would return for giving herself to laying eggs. In a state of nature such an unbalanced development of the powers that should coöperate in the process of reproduction could never have become so marked; for the one-sided development of any individual causing it to produce even a few eggs or young in excess of the normal number would in some degree impair its power of leaving successful offspring. The failure of such individuals to leave their full proportion of offspring, and the effect of this failure on the race, I describe as the action of filio-parental selection setting limits to the range within which fecundal selection may act.

11. *Fecundal Selection in Human Races.*

One of the most striking examples of the loss of fertility, and of the gradual extinction that follows, is found in the experience of the Polynesians since their contact with Europeans. In but few of the islands of the Pacific have the aborigines been displaced by conflict of arms or by industrial competition. The great cause of their disappearance, during the earlier periods of intercourse was their inability to cope with the microbes of measles, smallpox, leprosy, and other diseases, unknown to them before the arrival of Europeans and Chinese. But in many groups of these islands, and especially in Hawaii, that stage of disadvantage is now largely past, through the protection gained from Western science. Still the steady decrease in numbers continues, for the birth rate is not sufficient to meet the natural rate of mortality. And there is no reason to attribute this small birth rate to poverty or to prudential selection. Whatever the antecedent causes may have been, the present condition is failure to meet the demands of fecundal selection.

The nature of the deficiency is more fully realized when the decrease of the Polynesian race in their original home is compared with the increase of the African race in North and South America.

12. *Statistical Methods in the Study of Fertility.*

Karl Pearson has within a few years published several interesting discussions on the subject of fertility as a factor in the evolution of civilized man,* in which he has reached by statistical methods some

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* See "Chances of Death and Other Studies in Evolution," Chapter III, entitled "Reproductive Selection," published by Edward Arnold, London and New York, 1897; also "The Grammar of Science," second edition, published by A. C. Black, London, 1900; in the sections devoted to reproductive or genetic selection.

of these results which I had previously reached by other methods. The points in which our results most fully correspond are that fertility tends to increase till checked by some other form of selection; that transformation of race may be produced by this principle; and that, in a species well adjusted to the environment, the typical form of the species is not only the best adapted, but it is the most fertile. Concerning "a tendency to increasing fertility in man," he says: "We can not doubt that reproductive selection would steadily tend to alter the mean fertility in man, unless it were somehow held stringently in check. It is a point which seems to me of the utmost significance that (as revealed by the statistics of 4,390 Anglo-Saxon families) allowing for the proportion of the unmarried in the population, about one-fifth to one-sixth only of the adults produce quite one-half of the next generation, and any correlation between inheritable (physical or social) characteristics and fertility must thus sensibly influence that next generation." (The Chances of Death, pp. 82, 83.) In regard to the transforming influence of this principle he says: "I think there is quantitative evidence that types of life may change without the action of organic or inorganic environment, *i. e.*, solely owing to something inherent in their constitution. One such factor of evolution, genetic selection, I shall refer to later." (The Grammar of Science, p. 376.) Of the relation of fertility to type he says: "For stable races there is a strong tendency for the character of maximum fertility to become one with the character which is the type." (The Grammar of Science, p. 444.)

The importance of applying statistical methods of investigation to the problems of human evolution can not be overstated; but, for the full success of these methods, it is necessary that the nature of the factors in their fundamental relations to each other should be clearly apprehended and clearly stated in the definitions of the terms by which the different influences are designated. This necessity seems to require that we should have some knowledge of the probable factors before we can even collect the statistics that will be of avail in giving a quantitative measurement of the effects of any one factor. We must have a clear conception both of the scope and of the limits of a given factor or we may ascribe to it effects that are produced by other factors, or ascribe to other factors effects produced by it. By way of illustration, we may ask what is the scope and what are the limits of the terms *fertility* and *reproductive selection* as used by Karl Pearson? When he says (The Chances of Death, p. 81), "Hence it would seem that any characteristic or organ—such, for instance, as stature or size of pelvis in the mother—correlated with fertility would be progressively changed, * * * owing to reproductive selection," we are led to suppose that reproductive selection depends in part on that fertility which depends on the fitness of the pelvis of the mothers for fulfilling the functions of pregnancy and parturition. We also reflect that in all mammalian mothers there are organs on the fitness of which for furnishing nourishment to the young must depend the success of the process of reproduction. Does this form of survival of the fittest (or failure of the least fitted to leave mature offspring) come under the principle of reproductive selection as defined by our author? Again, we know that, in the case of many species, the males who are best fitted for driving off rivals, or who are best fitted for attracting the females, leave the most offspring. Is their success in reproducing an example of reproductive selection? According to Darwin's nomenclature this process is called sexual selection; but Karl Pearson's definition of sexual selection is: "All differential mating due to taste, habit, or circumstance, which prevents a form of life from freely intercrossing. If this goes on for a sufficient period during which differentiation of type is in progress, the principle of correlation may account for a sufficient differentiation in reproductive organs or functions to render intercrossing physiologically or mechanically difficult, distasteful, or even impossible, and accordingly give rise to the relative or absolute sterility of the differentiated types, *i. e.*, to the origin of species." (Grammar of Science, p. 418.) It is very pleasant to find such full recognition of the principle of isolation, even though it be under another name; but the question at present is, where does he place the survival through successful propagation of those who are best able to win partners? Does he classify it as a form of natural selection, or as a form of sexual selection, which has been so defined as to be equivalent to isolation; or is it included under reproductive selection? After reading the passage already quoted from page 81 of The Chances of Death, the last of these three suppositions seems the most probable; and still more so after reading the following definition of reproductive selection given on pages 65 and 66:

> If there be any sensible correlation between fertility and the size of any organ or intensity of any characteristic in male or female—that is, if deviations in excess (or defect) from the mean of this organ correspond to a greater fertility than deviations in defect (or excess)—then under the action of heredity we have a *vera causa* of progressive evolution in this organ; for an increasing number of individuals will be born with the organ in excess (or defect), and consequently the mean, and most probably the variation about the mean, of the general population will be progressively modified. The result is somewhat similar to that due to artificial selection in the case of domestic animals, where without extermination greater fertility is given to selected parents by pairing them only, or by pairing them more

frequently than others. In a memoir on Regression, Heredity, and Panmixia, recently published, I have ventured to term this possible factor of progressive evolution "reproductive selection."

This definition seems very definitely to include not only sexual selection but the forms of reflexive selection which I have called social, filio-parental, dominational, and impregnational selection. But we can have but little confidence that we have reached the correct interpretation of the meaning he would have us give to the terms "reproductive selection" and "fertility," for when we come to the concluding sentence of the chapter, on page 102, we read: "In civilized man the survival of the fittest appears to be replaced by the survival of the most fertile," which seems to imply that fertility as he uses it does not depend on fitness.

13. *The Importance of Impregnational Isolation.*

The prevention of crossing between groups produced by the different forms of impregnational isolation is connected with several problems of great interest. After referring to the terms *segregate survival*, *segregate union*, and "physiological isolation," under which some of these principles have been grouped, we will consider certain of these problems.

(1) *Segregate survival* has presented itself to my mind in five aspects, namely: *Segregate fecundity, vigor, adaptation, freedom from competition*, and *escape from enemies*.

These are the influences that give emphasis to the importance of any form of positive segregation by which those of any one kind are brought together and enabled to breed together. It may at first seem that these are simply the forms of selection that are producing transformation within the different intergenerating groups. It is, however, quite otherwise; for diversity of selection may exist in full force in two adjoining districts, and partial positive segregation may exist between the two groups of a species occupying these districts; but, if the mixed unions are as fertile as the pure unions, and produce young as successful in surviving as those produced by the pure unions, the probability is that the two groups will not become increasingly divergent.

Impregnational isolation has now been presented under eight forms, of which the first three rest on morphological and physiological incompatibilities preventing or interfering with mixed unions, which may, therefore, be called *segregate union*. The second group of five forms rests on incompatibilities preventing either the normal fruitfulness of mixed unions or the power of the young thus produced to reach the ratio of individual survival and reproduction reached by the young of the pure unions, which may, therefore, be called segregate survival. Segregate union and segregate survival are forms of negative segregation; for without the aid of other influences they can not bring the compatible individuals into relations producing pure unions.

Segregate union includes dimensional, structural, and potential segregation, and it is of no small interest to note that the free and abundant distribution of the fertilizing elements of the different types, when coöperating with any one of these, secures conditions necessary for pure unions. This coöperation, therefore, produces positive segregation as truly as do sexual and social instincts that bring together those of one race.

(2) *Physiological selection* is so defined and described by Romanes as to include three of these eight forms of impregnational segregation. The three forms thus grouped are potential segregation, segregate fecundity, and segregate vigor. In his last book he uses "physiological isolation" to cover the same principles wherever they occur, reserving physiological selection for cases concerned in the origination of specific types.* I greatly prefer the term physiological isolation to physiological selection, for it seems to me that selection should be used for the superior success of forms that are both competing and freely intergenerating, and not to designate isolative principles.

(3) *Four classes of self-cumulative endowments.*—Before discussing these principles of negative segregation, through which the influence of positive 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) opening of new opportunities and independent possibilities through segregation; (3) special adaptation to present circumstances; (4) powers of multiplied individualization. Darwin has considered at length the first and the third, 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 vigor* 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

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* See Darwin and After Darwin, Part III, p. 9.

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 both belong in different degrees to members of the same intergenerant that are equally fitted. The cumulation of vigor, 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. The increase of segregative endowments and of fertility when coöperating is due to principles quite different from this, and differing from each other. The segregative endowments augment through the inherent tendency of those more highly endowed in this respect to breed exclusively with those of the same form, and, therefore, in the long run to segregate from others; while the fertility of the more fertile neither prevents the individual success of 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. Vigor 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, though they are adapted to conditions lying in the environment. Adaptation increases through the breeding together of the better adapted, resulting from the failure of the less adapted individuals to live and thrive. 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. 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,* through fecundal selection. 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. *Fecundal selection coöperating with natural selection insures, in the descendants, the predominance of the better adapted of the more fertile, and the more fertile of the better adapted.*

(4) *Partial positive segregation may be greatly strengthened by coöperating negative segregation.*—It seems to be a fundamental law that vigor 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 vigor 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 vigor and variation there is liable to come a time when some variety, inheriting sufficient vigor 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, when positive segregation is correlated with segregate fecundity, the segregated types tend to become more and more dominant in number; but, in the very nature of things not only will the segregation be for many generations only partial, but partial segregation—unless it is aided by some other principle—although it may greatly delay the submerging of different groups in one common group, will never prevent that result being finally reached. Though the siphon which 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 leveling 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 coöperation of segregate fecundity with partially segregative endowments 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 that 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 vigor"; that is, the highest fertility is attained when varieties are crossed and the vigor 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.*

(5) *Negative segregation unaided by positive segregation tends to extinction.*—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 coöperating with positive segregation, it will be in place to show that it is of itself only a negative form of segregation, having no power to insure the propagation of 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, first, that a male and a female each of several allied but mutually sterile species are brought together on one small island, all tendencies to positive segregation being removed, while mutual sterility still remains; second, that a male and female when once mated remain together for the breeding season; and, third, that all find mates. Now, if we have seven 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

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* See first edition, p. 238; fifth edition, p. 259; sixth edition, p. 258.

numerators are found in the seventh line of a table of figures which I call the "permutational triangle."* If we have ten 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, 1 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.

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 positive segregation can not 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 positive 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 positive segregation is aided by segregate fecundity, or by some other form of segregate survival.

(6) *Partial positive segregation unaided by negative segregation can not prevent fusion.*—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 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 produce pure-breeds as contrasted with the proportion of cross-breeds that

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* See Appendix II of this volume.

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.

Taking formula (4), reached a little below (on page 105), it will be seen that if $M = m$, that is, if cross-breeds are as fertile as pure-breeds, the ratios of cross-breeds to pure-breeds increases with each generation, and in time the pure-breeds will be overwhelmed.

14. *Segregate Freedom from Competition and Segregate Escape from Enemies.*

Before leaving the subject of segregate survival it may be well to give an illustration of the effects of these two forms of the principle when coöperating with industrial and social segregation. On certain of the South Pacific islands there are found two species of rats occupying the same areas; but one species has strong legs and claws fitted for climbing the trees which they inhabit, while the other species lives on the ground and has limbs fitted for its separate sphere of activities. As the latter is the prevalent type on surrounding groups of islands, there seems to be good reason for believing that the tree species was derived from the ground species.

Let us now consider some of the conditions that might easily arise in the formation of such a species. Let us first suppose that there arises a period of scarcity in which the ordinary food of the species is obtained with difficulty, while on the trees are to be found either fruits which are more or less accessible to a good climber, or perhaps snails, which in tropical regions live constantly on the trees of the dense forests. Again, let us suppose that the ordinary rat of the original stock finds his strength sufficient to enable him to spend only one-tenth of each day seeking food in the trees, and that accordingly he can do better by remaining on the ground; but there are a very few individuals, say one in a thousand, who are able to spend one-quarter of their time in climbing; and for them there is abundance of food, which induces them to spend most of their time in the trees. These few find holes in the trees, where they congregate during hours of rest, and thus become more or less segregated from the rest of the species.

Again, let us assume that half of these rats feeding in the trees are of variation a, with instincts leading them to spend one-half of their time in the trees and one-half of their time on the ground, the result being that one-half of them form cross unions and have their nests on the ground, while one-half of them pair with tree-feeding rats and have their nests on the trees. Further, let us assume that the fertility of the pure-breeds and half-breeds is the same, each pair producing about 80 young during their life. Therefore, the multiplier for the pure-breeds, which in my tables is represented by M, is 40; and the multiplier for the half-breeds is also 40, *i. e.*, $m = 40$. And once more, let us assume that of the cross-breeds which have their homes on the ground with the original stock only 1 in 40 reaches maturity; that is, on account of the number of their enemies and the severity of the competition for food, their real multiplier, after all the conditions of survival have had a chance to operate, is $40 \times \frac{1}{40} = 1$. In other words, the original stock and the half-breeds mingled with them are simply able to hold their own, without any continuous increase. On the other hand, the arboreal group are so free from enemies and so well provided with food that three-fourths of them come to maturity, and their multiplier when corrected is $40 \times \frac{3}{4} = 30$.

Let us assume that the other half of these rats feeding on the trees are of the variation *b*, with instincts leading them to spend one-third of their time on the ground, and accordingly one-third of them mate with the original stock and have their nests on the ground. As in the case of variation *a*, the multiplier for pure arboreal breeds is 30 and for cross-breeds is 1.

Let us now suppose that there is an arboreal colony of 60 individuals occupying a forest on one of these islands, and that 30 of them belong to the variation *a*, and 30 of them to variation *b*. What will be the number of pure-breed arboreal rats in the next generation, and of these how many will be the offspring of variation *a* and how many the offspring of variation *b*?

Of variation *a* one-half cross with the original stock and we have—

Cross-breeding offspring, $15 \times 1 = 15$.
Pure-breed offspring, $15 \times 30 = 450$.

Of variation *b*, one-third cross, and we have—

Cross-breed offspring, $10 \times 1 = 10$.
Pure-breed offspring, $20 \times 30 = 600$.

Therefore, in the next generation of the pure-breed colony in the trees there will be 1,050, of which three-sevenths are offspring of variation *a* and four-sevenths are offspring of variation *b*. It follows that through hereditary influences the average instinct for arboreal life will be increased; and we may expect it to continue to increase in the same way in successive generations.

But there is a psychological influence that will come in to exaggerate the segregative tendency. The 1,050 rats of the generation we have now reached have been reared on the trees of the dense forest or jungle, where they may travel over a considerable area without descending to the ground, and have formed the habit of spending their whole time in the trees, so that not 1 in 100 will mate with the ground rats; and in a few more generations this ratio will become only 1 in 1,000, or 1 in many thousands. Under such conditions the arboreal variety will soon develop a manner and movement by which they recognize each other; and their social instincts will lead them to band together in driving away the rare intruders from the ground who venture to invade their sphere of influence. Their isolation from the original stock may thus become complete in the course of a few generations, and that, too, without any action of the principles of segregate fecundity and segregate vigor; that is, without the coöperation of any form of what Romanes has called "physiological segregation."

Segregate freedom from competition and segregate escape from enemies favor segregation in the earlier stages of newly adopted methods of life, and so tend to exaggerate the importance of slight changes attained by the first stages of divergent forms of environal selection. When the new colony has so multiplied as to appropriate nearly all the newly opened resources, competition will again become an important factor, and by that time the gradual appearance of segregate fecundity and segregate vigor may fortify the new type against being swamped by crossing. Segregate adaptation is also an important factor coöperating in the whole process. So the five principles of segregate survival are found to sustain and supplement each other in producing divergent evolution.

15. *Computation of the Ratio of Cross-breeds to Pure-breeds, under Given Ratios of Mixed Unions and of Fertility.*

It will simplify the problem if individuals of different degrees of crossed descent are classed together and compared with those of pure descent. It will also be a convenience to make M = the multiplier that represents the influence of all the conditions of survival for those of pure descent, and m = the multiplier that represents the influence of all the conditions of survival for those of mixed descent. A = the initial number of the new variety; c = the fraction that represents the proportion of the pure-breed individuals that form cross-unions; and P = the whole number of individuals of pure descent. C = the whole number of individuals of cross descent.

It may be observed that a problem of completely parallel terms will be obtained if we make A = an initial number of dollars left as an endowment to draw compound interest for many years; c = a rate of taxation corresponding in its periods with the periods for estimating interest, the avails of this taxation being kept for another institution. M = the multiplier by which we obtain the principal plus the interest remaining in the endowment; m = the multiplier by which we obtain the principal plus the interest allowed on the money withdrawn by taxation; $P =$ the whole value of the endowment at the end of a given number of periods; $C =$ the whole of the money withdrawn by taxation and subjected to a separate rate of interest, down to a given period.* It should be observed that, as in the bionomic problem M and m are liable to become fractions less than 1, so also in the problem of money investment either of these factors may fall below 1. This is the case when the charges for management, etc., are more than the interest.

Table giving Formulas for the Ratios between Cross-breeds and Pure-breeds.

In third generation, $P = A\ (M - Mc)^3 =$ pure-bred individuals in the third generation.

In nth generation, $P = A\ (M - Mc)^n =$ pure-bred individuals in the nth generation.

$C =$ the number of cross-bred individuals in any generation.

In first generation:

$$C = Acm$$

In second generation:

$$C = Acm^2 + Acm\ (M - Mc)^1$$

In third generation:

$$C = Acm^3 + Acm^2\ (M - Mc)^1 + Acm\ (M - Mc)^2$$

$$= Acm\ (M - Mc)^2 \left\{ \left[\frac{m}{M - Mc}\right]^2 + \left[\frac{m}{M - Mc}\right]^1 + 1 \right\} \dagger$$

In nth generation:

$$C = Acm\ (M - Mc)^{n-1} \left\{ (\ )^{n-1} \ldots (\ )^3 + \left[\frac{m}{M - Mc}\right]^2 + \left[\frac{m}{M - Mc}\right]^1 + 1 \right\}$$

In third generation:

$$\frac{C}{P} = \frac{mc}{M - Mc} \times \left\{ \left[\frac{m}{M - Mc}\right]^2 + \left[\frac{m}{M - Mc}\right]^1 + 1 \right\}$$

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* The method by which the first steps are made in reaching the desired formula will be understood by considering this endowment problem. The advantage of the formula here reached is that it gives the ratio of all the cross-breeds to pure-breeds, and not simply of half-breeds to pure-breeds, as was the case in the formula reached in my paper on Divergent Evolution (see Appendix I).

† This is obtained by dividing each term of the second member of the previous equation by $Acm\ (M - Mc)^2$, and then placing the same amount as a multiplier outside of brackets.

In nth generation:

$$\frac{C}{P}=\frac{mc}{M-Mc}\times\left\{\left[\frac{m}{M-Mc}\right]^{n-1}+\,..()^3+\left[\frac{m}{M-Mc}\right]^2+\left[\frac{m}{M-Mc}\right]^1+1\right\}$$

As the sum of the above progression within the brackets is found by the formula $S=\frac{a}{1-r}$ in which $a=1$ and $r=\frac{m}{M-Mc}\therefore$

$$\frac{C}{P}=\frac{mc}{M-Mc}\times\frac{1}{1-\dfrac{m}{M-Mc}}=\frac{mc}{M-Mc}\times\frac{M-Mc}{M-Mc-m}$$

$$\therefore\quad\frac{C}{P}=\frac{mc}{M-Mc-m}=\text{Formula (3)};^*$$

and

$$C=P\times\frac{mc}{M-Mc-m}=\text{Formula (4)};$$

TABLE A.

[From Formula (4).]

When M = 10 and m =	9.	8.	7.	6.	5.	4.	3.	2.	1.
If $c=\frac{1}{2}$, then cross-breeds = pure-breeds ×	$\frac{9}{-8}$	$\frac{8}{-6}$	$\frac{7}{-4}$	$\frac{6}{-2}$	$\frac{5}{0}$	$\frac{4}{2}$	$\frac{3}{4}$	$\frac{2}{6}$	$\frac{1}{8}$
If $c=\frac{1}{3}$, then $C=P\times$	$\frac{9}{-7}$	$\frac{8}{-4}$	$\frac{7}{-1}$	$\frac{6}{2}$	$\frac{5}{5}$	$\frac{4}{8}$	$\frac{3}{11}$	$\frac{2}{14}$	$\frac{1}{17}$
If $c=\frac{1}{4}$, then $C=P\times$	$\frac{9}{-6}$	$\frac{8}{-2}$	$\frac{7}{2}$	$\frac{6}{6}$	$\frac{5}{10}$	$\frac{4}{14}$	$\frac{3}{18}$	$\frac{2}{22}$	$\frac{1}{26}$
If $c=\frac{1}{5}$ then $C=P\times$	$\frac{9}{-5}$	$\frac{8}{0}$	$\frac{7}{5}$	$\frac{6}{10}$	$\frac{5}{15}$	$\frac{4}{20}$	$\frac{3}{25}$	$\frac{2}{30}$	$\frac{1}{35}$
If $c=\frac{1}{6}$, then $C=P\times$	$\frac{9}{-4}$	$\frac{8}{2}$	$\frac{7}{8}$	$\frac{6}{14}$	$\frac{5}{20}$	$\frac{4}{26}$	$\frac{3}{32}$	$\frac{2}{38}$	$\frac{1}{44}$
If $c=\frac{1}{10}$, then $C=P\times$	$\frac{9}{0}$	$\frac{8}{10}$	$\frac{7}{20}$	$\frac{6}{30}$	$\frac{5}{40}$	$\frac{4}{50}$	$\frac{3}{60}$	$\frac{2}{70}$	$\frac{1}{80}$
If $c=\frac{1}{100}$, then $C=P\times$	$\frac{9}{90}$	$\frac{8}{190}$	$\frac{7}{290}$	$\frac{6}{390}$	$\frac{5}{490}$	$\frac{4}{590}$	$\frac{3}{690}$	$\frac{2}{790}$	$\frac{1}{890}$
If $c=\frac{1}{1000}$, then $C=P\times$	$\frac{9}{990}$	$\frac{8}{1990}$	$\frac{7}{2990}$	$\frac{6}{3990}$	$\frac{5}{4990}$	$\frac{4}{5990}$	$\frac{3}{6990}$	$\frac{2}{7990}$	$\frac{1}{8990}$

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* Formulas (1) and (2) were given in my paper on Divergent Evolution (see Appendix I).

Method of Testing Table A.

Let $M = 10$; $m = 7$; $c = \frac{1}{4}$; then $\frac{C}{P} = \frac{7}{2}$ according to the table.

We now place under pure-breeds any number, and under cross-breeds $3\frac{1}{2}$ times that number.

Pure-breeds.	Cross-breeds.	$\frac{C}{P}$
In *n*th generation, 2	In *n*th generation, 7	$\frac{7}{2}$
$(n+1)$th " $= 2(M - Mc)^1 = 15$	In $(n+1)$th gen., $49 + \frac{7}{2}$	$\frac{7}{2}$
$(n+2)$th " $= 2(M - Mc)^2$ $\left.\right\} = \left\{ \begin{matrix} 2(7.5)^2 \\ = 2(56.\frac{1}{4}) \end{matrix} \right\} = 112\frac{1}{2}$	$\left\{ \begin{matrix} 7^3 + \frac{7^2}{2} + \left[\frac{15}{4} \times 7\right] \\ = 343 + 24\frac{1}{2} + 26\frac{1}{4} \end{matrix} \right\} = 393\frac{3}{4}$	$\frac{7}{2}$

Starting with the fraction $\frac{7}{2}$, given in Table A, as correct for the *n*th generation, we find that $\frac{C}{P} = \frac{7}{2}$ is correct for all subsequent generations; and this proves the formula to be correct.

If the denominator of the fraction representing the value of $\frac{C}{P}$ is 0, or less than 0, the disproportion increases with each generation; that is, cross-breeds become the overwhelming element.

In this case by which we are testing the correctness of Table A, suppose the pure-breeds to be 2 and the cross-breeds to be 7 in the generation with which we commence. In the next generation, which we designate as the $(n + 1)$th generation, the pure-breeds will be $2 \times (M - Mc)^1 = 2\left[10 - \frac{10}{4}\right] = 15$. In the $(n + 2)$th generation the pure-breeds $= 2 \times (M - Mc)^2 = 2 \times (7.5)^2 = 112.5$.

The cross-breeds in the $(n + 1)$th generation $= 7 \times$ the cross-breeds of the previous generation, plus $7 \times$ one-quarter of the pure-breeds of the previous generation $= 7^2 + \frac{7}{2}$. In the $(n + 2)$th generation the cross-breeds will be $7 \times$ the cross-breeds of the $(n \times 1)$th generation, plus $7 \times$ one-quarter of the pure-breeds of the $(n + 1)$th generation $= 7^3 + \frac{7^2}{2} + \left[\frac{15}{4} \times 7\right] = 393.75$.

16. *The Use of the Tables.*

The first object of this computation is to show that a partial positive segregation that is ineffectual in preserving a new variety from the swamping effects of crossing becomes very effectual when a moderate degree of segregate fecundity coöperates with it. It should be observed that when considering partial segregation coöperating with segregate fecundity I assume that the two varieties that are competing on the same area are equally adapted to the environment, and that the action of other principles is equal in each, in order that I may compute the effects of the two factors under consideration when free from disturbing influences. It has been objected that, according to my Table I,* the eighteenth generation is many thousand times larger than the initial number, which is not the usual result under the conditions surrounding natural varieties. In reply I would say that even in natural varieties it is not at all impossible that the number should double with each generation for at least a few generations, especially when a variety has gained the use of resources heretofore unused, and that for the purpose of showing the ratio in which half-breeds and pure-breeds stand to each other it is entirely immaterial whether we assume that the number that arrive at maturity are the same in each generation, or that each successive generation is nearly double that of the preceding generation.

But does not the assumption that the ratio of cross-breeding remains the same in successive generations vitiate the whole computation and render it worthless? I think not. My contention is that when segregate fecundity comes to the aid of such a principle as prepotential segregation (which is only partial in its action, and therefore by itself unable to prevent swamping), the result is the progressive action of both principles in each successive generation. But before we can show how this cumulative action arises we must have some formula for showing the natural result of any given degree of segregation combined with a given degree of segregate fecundity; and the proper formula for this purpose seems to be the result that would be reached, if the principles should continue at the given degrees for a considerable number of generations.

Take for example the case represented in Table I.* What is the ratio between half-breeds and pure-breeds that most truly represents the case? Shall we go to the end of the first generation and say that, $\frac{H}{P}=\frac{1}{18}$, or go to the eighteenth generation and find that $\frac{H}{P}=\frac{1}{10}$?

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* See my paper on Divergent Evolution, Appendix I.

Undoubtedly the latter is the one we need to represent the result toward which the given conditions tend, though before the eighteenth generation is reached the degree of segregate breeding will have become more stringent.

Having obtained a formula giving the results that would be reached if the ratios of cross-breeding and of attendant infertility were continued at a given level for a number of generations, we next inquire whether there is any reason to believe that the degrees of segregate breeding will become more stringent in successive generations, and whether the infertility of cross-breeds will be increased.

17. *Cumulative Segregation Resulting from Segregative Endowments.*

Let us consider a partially segregated variety of a plant species in which there is some variation in the segregative endowments. We will suppose that the species is one whose pollen is freely distributed by the wind and whose stigma is susceptible of fertilization for ten hours.

Though the individuals of the new and partially segregated variety are very few as compared with the original stock, yet the pollen of the new kind reaches every stigma of the same kind before the ten hours of its susceptibility have passed, while pollen of the original kind, being far more abundant, is sure to reach every stigma soon after their flowers have opened.

The positive segregation of the new variety we will suppose is secured by prepotence of the pollen of the variety on the stigmas of the same variety, one variation being prepotent for about five hours, with the result that one-half of the individuals breed pure and one-half are crossed; that is, $c = \frac{1}{2}$; while another variation is prepotent for about $6\frac{2}{3}$ hours, with the result that two-thirds of the individuals breed pure and one-third are crossed; that is $c = \frac{1}{3}$.

The negative segregation of the new variety we will suppose is secured by segregate survival; for the pure-breeds, through different degrees of adaptation to the new station, enjoy different degrees of success in leaving offspring that come to maturity, the less adapted variations being multiplied by 1 in each generation, and the better adapted multiplied by 2 in each generation, while the cross-breeds are so lacking in adaptation as to be multiplied by $\frac{1}{5}$ in each generation. We therefore have two values for M, each occurring under $c = \frac{1}{2}$, and again under $c = \frac{1}{3}$. In one variation we have $M = 1$, and $m = \frac{1}{5}$, the proportion being as $M = 10$, and $m = 2$; and in the other variation we have $M = 2$, and $m = \frac{1}{5}$, the proportion being as $M = 10$ and $m = 1$.

Solution reached by means of Table V.—Looking in Table V,* we find that when $c = \frac{1}{2}$, and $M = 10$,

(*var.* 1) then with $m = 2$, half-breeds = pure-breeds × $\frac{2}{10}$;
(*var.* 2) and with $m = 1$, half-breeds = pure-breeds × $\frac{1}{10}$;

that when $c = \frac{1}{3}$, and $M = 10$,

(*var.* 3) then with $m = 2$, half-breeds = pure-breeds × $\frac{2}{18}$;
(*var.* 4) and with $m = 1$, half-breeds = pure-breeds × $\frac{1}{19}$.

Now, it is evident that the influence on the next generation of the variation marked as *var.* 4, which is the most highly segregated, will be much greater than that of any other one of the variations.

Solution reached by means of Table A.—If we consult Table A, we shall find an equal contrast, for it gives for

(*var.* 1) cross-breeds = pure-breeds × $\frac{2}{6}$;
(*var.* 2) cross-breeds = pure-breeds × $\frac{1}{8}$;
(*var.* 3) cross-breeds = pure-breeds × $\frac{2}{14}$;
(*var.* 4) cross-breeds = pure-breeds × $\frac{1}{17}$.

Solution reached by direct computation.—A similar conclusion may be reached by computing the result for a few generations. Let us suppose that for one-half of the new variety the average prepotence allows one-half of the individuals to form cross-unions, and that for the other half of the variety the average prepotence allows only one-third of the individuals to form cross-unions; and also that one-half of each of these variations is so adapted as to multiply by 2 in each generation, while the other half multiplies by 1. As in the previous computation cross-breeds are multiplied by $\frac{1}{5}$ in each generation. Let us now assume that in a given generation there are 1,000 individuals in each of these variations, and what will be the number of pure-breeds of each of the four variations that will come to maturity in the next generation, and what the number of cross-breeds?

In *var.* 1, $c = \frac{1}{2}$, $M = 1$, $m = \frac{1}{5}$; (*i. e.*, pure-breeding 500; crossing 500), . . pure-breeds 500; half-breeds 100.

In *var.* 2, $c = \frac{1}{2}$, $M = 2$, $m = \frac{1}{5}$; (*i. e.*, pure-breeding 500; crossing 500), ∴ pure-breeds 1,000; half-breeds 100.

In *var.* 3, $c = \frac{1}{3}$, $M = 1$, $m = \frac{1}{5}$; (*i. e.*, pure-breeding 666; crossing 333), ∴ pure-breeds 666; half-breeds 66.

In *var.* 4, $c = \frac{1}{3}$, $M = 2$, $m = \frac{1}{5}$; (*i. e.*, pure-breeding 666; crossing 333), ∴ pure-breeds 1,332; half-breeds 66.

The sum of the pure-breeds of all the variations 3,498.

It will be observed that in one generation the pure-breeds have decreased from 4,000 to 3,498; that is, their numbers have dimin-

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* See my paper on Divergent Evolution, Appendix I.

ished one-eighth. In the second generation the result will be quite different; for variations 2 and 4 already constitute two-thirds of the whole number of pure-breeds.

Second Generation—	Pure-breeds.
Of variation 1	250
Of variation 2	1,000
Of variation 3	444
Of variation 4	1,776
	3,470

In this generation the decrease is only 28 individuals, or about $\frac{1}{125}$.

Third Generation—	Pure-breeds.
Of variation 1	125
Of variation 2	1,000
Of variation 3	296
Of variation 4	2,368
	3,789

In this generation there is an increase of 319 individuals, or a little over $\frac{1}{11}$.

Fourth Generation—	Pure-breeds.
Of variation 1	62
Of variation 2	1,000
Of variation 3	198
Of variation 4	3,156
	4,416

In this generation there is an increase of 627, or of nearly $\frac{1}{6}$.

Tenth Generation—	Pure-breeds.
In variation 1	0.98
In variation 2	1,000
In variation 3	16
In variation 4	17,758
	18,775

Var. 4, of *Tenth Generation* $= 1{,}000\,(1.3333\frac{1}{3})^{10}$ computed by logarithms.

We therefore observe that in the tenth generation variation 1 has become less than 1, and variation 4 has become the predominant type.

For the next ten generations the average positive segregation will be advanced, (1) by the preponderance of variation 4, and (2) by the fact that the new variety occurs in much larger masses than at the beginning of the computation, and will therefore be less exposed to cross-fertilization.

Now that the mass of pure-breeds is increased more than fourfold, it is reasonable to suppose that the ratio of pure-breeding advances.

We may also assume that increased segregate fecundity and vigor will make the multiplier for pure-breeds = 2, and the multiplier for cross-breeds $= \frac{1}{10}$. And when another ten generations have passed, still higher degrees of segregation will be the natural result.

Conclusion.—We have now approached in three different ways the proof of cumulative advance in a set of innate qualities, which by their combined action produce in moderate degress both positive and negative segregation. The result seems to be that when M by any chance comes to be larger than $Mc + m$, then the fraction $\frac{mc}{M - Mc - m}$, which gives the ratio of cross-breeds to pure-breeds,* becomes a positive quantity, and a given proportion of the whole stock remains unaffected by crossing. This point having been reached the subsequent tendency is toward a constant increase in the segregative endowments.

18. *Institutional and Prudential Selection.*

Institutional and prudential selection stand in the same relation to the other forms of reflexive selection that artificial selection holds in relation to natural selection. They are the forms of reflexive selection established in communities of rational beings for the purpose of securing ends that are more or less fully apprehended as the goal.

It should be observed that inherited instincts have an important part in each of the forms of conjunctional selection, that is, in *sexual*, *social*, and *filio-parental selection;* and again in the forms of impregnational selection and impregnational isolation just discussed, the coördinations are due to inherited characters, either morphological or physiological; but in institutional and prudential selection the processes are guided by conscious and reflective purpose. It will, therefore, be seen that the conscious regulation of relations between husband and wife, between man and man, or between parents and children, when it affects the form of survival, belongs to either institutional or prudential selection, and not to conjunctional selection in any one of its three forms. In the past history of man the three forms of conjunctional selection have been of prime importance; but as civilization advances increasing control is given to institutional and prudential selection. Moreover, in the case of civilized man, dominational selection through intra-group struggle has in a large measure ceased to be a struggle for life or for the opportunity to have a full share in producing the next generation, and has become chiefly a struggle for influence in society and for escape from certain forms of

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* See Formula (4), on page 105.

drudgery. If degeneracy is threatened, the remedy will not be found in restoring the conditions of savage life, in which the imbecile and the insane, the deaf and the diseased, are all eliminated by starvation; but rather by such forms of institutional and prudential selection, enforced by public opinion and law, as will prevent the marriage of those who are specially liable to have defective offspring. It thus appears that institutional selection and prudential selection, both of which may be subjected to rational control, are the chief factors by which man may hope to maintain and control his own evolution.

The powerful influence of institutions on human evolution will be recognized by those who consider the effects that must be produced on the vigor and vitality of a nation when military organization and destructive wars prevent many of the most vigorous men from having any share in producing the next generation, while many others who leave children are suddenly removed by death when their families most need their aid. Again, the institutions in which the community combines for the maintenance of justice and order and the training of the young must have a profound influence on the physical inheritance of the race, through the advantage it gives to the peaceful and law-abiding.

In the evolution of civilized man the law of natural increase is liable to be set aside in a way that often becomes extremely abnormal. I refer to the effects of *prudential selection* in limiting the size of families, both by delaying marriage and by restraint after marriage. Of course, both methods of using the reason are legitimate if the end sought is not a selfish desire to be free from care and responsibility. The evil has grown to such proportions in certain communities that the very existence of these groups is threatened. The fundamental difficulty seems to be that public opinion has failed to set before the men and women of force and character—before those who are the backbone of the nation—the double ideal of maintaining a vigorous life and civilization during their own generation and of transmitting the same to a posterity of unabated vigor and of high native character, as well as of high training and culture. It is impossible that this standard should be attained if there is unwillingness to establish family relations until the battle of life has been fought out and won. Nor can it be realized if after marriage those who should become parents wish to reserve the chief portion of their energy for social entertainments or for the pleasures of art, science, literature, and travel, with no consideration of how these great gifts of past generations can be best transmitted and rendered continuously progressive in the hands of those who are capable of receiving, maintaining, and transmitting the same.*

This factor is probably having a profound influence on the present evolution of the most highly civilized nations. In his volume on The Chances of Death, Karl Pearson says in a note (see p. 83):

> Mr. Francis Galton tells me that he was recently informed by credible medical authorities in Paris that the French population is becoming Breton, owing to the fact that this element of the population does not limit its fertility to anything like the same extent as other elements. Nearly all large families are found to be of Breton extraction.

Similar changes of population are taking place in New England and in other countries, and in some of these cases the cause is probably the one we are now considering. The continuance of any human race depends not only on its power to produce vigorous and adapted offspring in sufficient numbers, but on its willingness to exercise this power and to assume the heavy responsibilities of rearing and training the young. If the Bretons are willing, and persist in being willing, France may become their inheritance; if they give way, the inheritance will pass to others. But the French are not the only people that are threatened by this selfish individualistic civilization. Its blighting effects are apparent among the professional and commercial classes in other countries. The statistics obtained by Karl Pearson, some relating to families of Anglo-Saxon extraction and others relating to Danish families, do not give the proportion of the same classes that remain unmarried; but careful analysis of the facts given leads him to remark:

> There are clear traces in the statistics of some special action influencing fertility in families with between 3 and 7 children. * * * It is noteworthy also that this characteristic is less marked in statistics drawn from pedigrees than in more recent natal statistics. I can not, therefore, avoid the conclusion that the dip between 3 and 7 is not due to compoundness; that its origin is comparatively recent, and that it is an artificial break in the natural smoothness of the curve of fertility. I believe it to be entirely due to a Malthusian restraint on population. Families which reach 7 and over appear to be those in which no check is placed on the "natural" growth. Below 7 there is a tendency to restraint which is

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* Since this paragraph was written Mr. Francis Galton has delivered the second Huxley lecture of the Anthropological Institute (of London), in which many suggestions are made for reversing the present unfavorable action of prudential selection. The lecture is entitled "The Possible Improvement of the Human Breed under the Existing Conditions of Law and Sentiment," and is published in "Nature" Oct. 31, 1901. In his view the high racial development of the most gifted fiftieth part of the human race is of more importance than the suppression of the lowest type, though he recognizes both methods as needed for reaching the best results.

marked by a transference of frequency from families which should lie between 4 and 7 to those lying between 0 and 4. * * * While the theoretical curve will be found to give only 6 to 8 per cent of marriages without issue, we find in modern statistics 11 to 18 per cent of marriages with no issue * * * and this even in countries like England and Denmark, where restraint is not usually supposed to be so prevalent as in France.*

Again, he remarks: "The prudential restraint on marriage and parentage in the more educated members of the community, which we are apt to regard as a social virtue, may after all have its dark side."†

19. *Institutional Election, Partition, and Isolation.*

Institutional election arises through the influence of public opinion giving prominence, influence, and success to individuals who conform most fully to the social standards of justice and propriety; and is reinforced by the law which puts a definite check on individuals whose actions fall so far below these standards that the community will not tolerate the offenders. Again, each community has its language, its industrial methods, its arts and sciences, and its forms of etiquette, which must be transmitted by tradition from generation to generation, for these attainments can not be transmitted by racial heredity, and their continuance in the community depends on example, education, and training on the part of the older generation, and on the part of the younger generation imitation, study, and practice. Now, institutional election includes the superior success and influence of the individuals who attain the most complete equipment in these acquired characters that belong to the community.

Institutional partition arises when local isolation and partition has resulted in divergence in language, religion, and education, preventing the possibility of association in one community when local isolation and partition has ceased.

Institutional isolation.—Again, the differences in language, religion, and education, which prevent free association, will also prevent free intermingling of race, and the result is institutional isolation. Examples of institutional partition and isolation are seen in the Mohammedan and Christian communities occupying the same regions in Turkey.

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* See Chances of Death and Other Studies in Evolution, pp. 67-69.

†*Ibid.*, p. 102.

CHAPTER VII.

ANALYSIS OF THE FOUR PRINCIPLES (CONTINUED).

I. THE METHODS OF THE ENVIRONAL MODE OF EACH PRINCIPLE, WITH THE FORMS OF EACH METHOD.

Producing demarcation of habitudinal groups:
- Environal partition.
  - Endonomic partition.
    - Industrial partition.
    - Migrational partition.
  - Heteronomic partition.
    - Transportational partition.
    - Geological partition.
    - Artificial partition.

Producing intensification of habitudinal groups:
- Environal election.
  - Endonomic election.
    - Habitudinal election.
    - Aptitudinal election.
  - Heteronomic election.
    - Natural election.
    - Artificial election.

Producing demarcation of racial groups:
- Environal isolation.
  - Endonomic isolation.
    - Industrial isolation.
    - Chronal isolation.
      - Seasonal isolation.
      - Cyclical isolation.
    - Migrational isolation.
  - Heteronomic isolation.
    - Transportational isolation.
    - Geological isolation.
    - Fertilizational isolation.
    - Artificial isolation.

Producing intensification of racial groups:
- Environal selection.
  - Endonomic selection.
    - Habitudinal selection.
    - Aptitudinal selection.
  - Heteronomic selection.
    - Natural selection.
    - Artificial selection.

Having completed our analysis of the methods and forms of the reflexive mode of influence, we will now briefly survey the forms of the environal mode. Under each or the four principles, when we find that the relations between the group and its environment are determined by conditions within the group, we call the influence endonomic selection, election, isolation, or partition, as the case may be; or if the relations are determined chiefly by conditions lying outside of the group, we then speak of the influence as heteronomic.

1. *Environal Selection and Environal Election.*

Environal selection, as we have just seen, may be either endonomic or heteronomic.

Divergent forms of endonomic selection often arise through divergent habitudes or aptitudes of the individuals starting the isolated colonies, or through the accidents attending the entrance of small groups into isolated *districts presenting the same environment.*—In my paper reproduced in Appendix II of this volume I have emphasized the fact that it is true of a very wide range of species that any one species distributed in small sections in several isolated districts, presenting the same environment, will often use the environment in different ways, and so be subjected to different forms of selection. Selection thus determined by the relations in which the organism puts itself to the environment I call endonomic selection.

We shall here consider in fuller detail the different conditions that may produce divergent forms of selection in isolated groups, exposed to the same environment. Let us first consider cases in which the isolated groups are very small, and from a species with many variations through adaptations to a complex environment, and in which the new districts to which they are brought present the same environment as is found in the original home of the species. That the conditions may be clearly apprehended, let us suppose that we are considering a species of Hawaiian tree-snails on the southwest side of the main mountain range of Oahu, confined to the shady groves of a single valley, shut in on either side and at the head of the valley by high ridges covered with open brush, and at the mouth of the valley by grassy slopes that extend to the sea. This snail lives continuously on the trees, clinging to the trunks and large limbs of five or six species, and presents many variations of color and some divergences in acquired habitudes according to the species of tree on which it has lived. If for many generations a certain strain should live entirely on one species of trees (perhaps occupying a single grove which includes no other trees), it would present innate aptitudes for that kind of life, developed by selection. Now, suppose that by some very rare accident a man, bearing a branch of a tree, unconsciously transports a single impregnated individual of this species of snail into the neighboring valley on one side, and within a few years a similar occurrence carries another individual of the same species, but occupying another kind of tree, into the valley on the other side. Each individual has occupied but one kind of tree for its whole life, and having formed habitudes strongly favoring the kind it has so far used, seeks and finds the same kind in the new district to which it has been brought. As there is no pressure of population in their new and previously unoccupied districts, the descendants of each remain for a hundred years or more in the grove in which the first comer settled down; and the two colonies have, perhaps for a hundred generations, been subjected to somewhat divergent forms of selection; for the habits of feeding have been different, and there has been no crossing between those of different habits, as was the case in the original home. This is an illustration of what I call "*habitudinal selection.*" We shall next consider an illustration of *aptitudinal selection*, which will be gained by changing the illustration just given at one point. Instead of taking the two individuals which start the two colonies from those which for a generation have been feeding on different kinds of trees, we must take them from two separate strains which have, for many generations, had their separate methods of feeding, so that not only their habitudes but their aptitudes must be somewhat different. Again, we may consider conditions that would produce what we might call "*accidental selcction.*" This might occur if the two individuals starting the two colonies were from the same strain and had both of them gained various experiences by feeding on different trees, so that their habits were not fixed. One of them we will suppose was brought by accident to a fine grove of candle-nut trees in the new district, and for a hundred years finds no cause to go elsewhere; while the other one, in another valley, is brought to a grove of what the Hawaiians call ohia trees, and there remains for an equal number of years. Is it not certain that the selection will be somewhat divergent; and to what determining cause shall we attribute the divergence if not to accidents that started these individuals of varied attainments in separate colonies, and in groves of different kinds of trees? As the valleys are near together and on the same side of the mountain range, the rainfall and other features of climate must be essentially the same. If the creatures under consideration were insects endowed with higher powers for exploring the environment, I recognize that accidents of the kind here suggested would have little or no effect in determining the forms of selection; for, in such cases, slight differences of aptitudes or habitudes would be sure to control the method of using the environment. Moreover, such species would not fall into isolated groups through their occupying separate valleys. When an isolated individual or pair deals with an environment possessing resources that are varied but familiar and easily explored, previous habitudes and aptitudes are the chief factors controlling the methods of using the environment. If the power of using different resources is great and the power of exploration small, the method of using the environment may be determined by the kind of resources first reached on entering the district.

Heteronomic selection is of two forms—*natural selection*, produced by conditions in the environment that are independent of any purpose to control the forms of survival, and *artificial selection*, which is determined by more or less distinct purpose to control survival. If in the case of the snails just considered some of them are brought to groves on the northeast side of the mountain range, they will be exposed to a somewhat greater rainfall, and will probably be subjected to some change through the resulting selection. Again, suppose a colony is planted on either side of the range, in a valley where but one kind of shade trees is found, and this a kind that has never before been occupied by the species. In both these cases we should have heteronomic selection of the form that has been called natural selection. If any of these snails should be discovered by man to be good for food or medicine, and should be subjected to selection for the purpose of improving the qualities sought, the result would be heteronomic selection of the artificial form.

Environal election corresponds with environal selection in the general influences by which it is shaped; but it differs in the results produced, for it relates to the intensifying of habitudes and acquired characters within the associating group. The higher the grade of intelligence the more marked are the changes and divergences introduced by acquired habitudes and characters, and accordingly, in such cases, *endonomic election* becomes the leading factor by which some new adjustment to the environment is developed into an established method of sustaining life; and if the inherited endowments are not in complete accord with the new life, coincident selection carries the adjustment to higher degrees; for variations favoring the conditions imposed by the new tradition will have the advantage. Examples of endonomic election preceding and introducing coincident selection are seen in the tree-climbing rats mentioned above,* and in the cats that have taken to wading and fishing.† *Heteronomic election* is either natural or artificial. *Artificial election* is seen in dogs and other domestic animals that have been subjected to training. *Natural election* is seen in the case of the chimney swift, which, in a large measure, having lost the hollow trees in which it used to build its nests, has been forced to find a substitute in the chimneys built by the intruders who cut down its trees. The new habit is undoubtedly being reinforced by instincts gradually established by coincident natural selection.

2. *The Methods of Environal Isolation.*

Endonomic isolation.—It is evident that, when varieties of the same species of plant occupying the same areas are prevented from crossing by flowering at different seasons, the process which I call seasonal isolation is rightly classed as a form of endonomic isolation. The

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* See page 101.

† See pages 67–68.

same is true of the cyclical isolation between two broods of the periodical cicada when occupying the same district.* As each brood lives nearly seventeen years burrowing in the ground, and then spends the few last weeks of its allotted life above ground breeding in the trees, it never has a chance to cross with the other brood, whose time for breeding comes on another year, and each seventeenth year thereafter.† *Industrial isolation* and *migrational isolation*, so far as they are determined by diversity in the habits or instincts of the members of the species, must also be classed as forms of endonomic isolation.

Heteronomic isolation.—In the four remaining forms of environal isolation, namely, transportational, geological, fertilizational, and artificial isolation, heteronomic influences must prevail.

3. *Industrial Isolation.*

Industrial isolation is isolation 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 isolation are sustentational, protectional, and nidificational isolation.

For the production of industrial isolation it is necessary that there should be, in the same environment, a diversity of fully and of approximately available resources more or less separated, 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 endeavor according to endowment. From the nature of the process it produces segregation; for those of like aptitudes are brought together.

It is evident that if initial variation presents in any case a diversity of adaptations to surrounding resources that can not be 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 abun-

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* For a full statement see U. S. Department of Agriculture, Division of Entomology, Bulletin No. 8, and Bulletin No. 14, New Series, 1898.

† For a comparatively full account of the different broods of this species, and the problems raised by the remarkable facts, see Appendix II, Sec. III, 3.

dant 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 individuals 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. When other forms of isolation arise, they may be entirely independent of change in the environment, the only change being in the forms or functions of the organism.

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 variation results in a slight difference in the kinds that succeed in germinating and in propagating in contrasted situations, we have diversity in the forms of natural selection affecting the seed, and the separation is what I hereafter describe as local isolation passing into local segregation. We therefore see that what I here call industrial isolation 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 are a multitude of cases in which endeavor 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 endeavor 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.

Again, endeavor, according to endowment, often secures separation according to endowment; and this gives an opportunity for the inheritable effects of diversity of endeavor (if there are such effects), to be accumulated in successive generations.

In the relation of endowment and endeavor we have a striking example of the peculiar interdependence of vital phenomena. Diversity of endowment is the cause of diversity of endeavor and of segregate breeding according to endowment, and segregate breeding according to endowment 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.

The effects of industrial isolation 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 isolation 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 competitive disruption, through the crowding of population inducing special efforts to find new resources, and leading to diversity of endeavor; and (2) that in either case the result is what is here called industrial segregation. In the first case, when the creatures are guided by some diversity of inherited instincts, the process is directly segregative, while in the second case it is primarily separative, but inevitably passes into segregate breeding. Divergence through diversity of use, and the resulting diversity of acquired characters, whether inherited or not, will operate as surely in the one case as in the other.

Sustentational isolation 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 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.

Protectional isolation is isolation 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 segregating 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 woodlands, while others might remain in their old haunt, gaining through protectional selection more and more likeness to some inedible species.

Nidificational isolation.—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 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 which at one time and in one place adopt the habit are usually sufficient to keep up the new strain if they succeed in securing the needed sustenance.

4. *Chronal Isolation.*

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

I distinguish two forms—cyclical and seasonal isolation.

Cyclical isolation is isolation 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 isolation is found in the case of *Cicada septendecim*, whose habitat is the northern portion of the Mississippi Valley and of the Atlantic States, though many outlying broods are found in other regions. The typical form has a life-cycle of seventeen years, but there is a thirteen-year race (*Cicada tredecim* Riley) found chiefly in the Southern States, and therefore separated from the typical form, both locally and chronally. As the life-cycle of this race is thirteen instead of seventeen years, in a district where the habitats of the two races overlap, even if there were no physiological or psychological incompatibility to overcome, interbreeding could occur between the two forms only once in 221 years, that is, once in 13 generations of the longer-lived race, and once in 17 generations of the shorter-lived race. The distribution of the two races in different districts seems to indicate that local isolation under different climatic conditions has had an important influence in their development. 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 isolation, which we consider in a following paragraph; but what is of special interest here as examples of complete cyclical isolation is the fact that in each of several limited districts there are found two broods of the same race whose appearance above ground is always separated by the same number of years.*

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 isolation 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 isolation is complete.

In such cases, so far as the time of maturing is concerned, the difference is segregative, while in every other respect it will be simply separative, except as separation passes into segregation. If the periodical cicada was as variable in form and color as is the Achatinella (as well as other genera of Hawaiian snails), we should probably find each brood characterized by easily recognized divergences.

Seasonal isolation is produced whenever the season for reproduction in any section of the species is such that it can not interbreed with other sections of the species. It needs no argument to show that if, in a plant species 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

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* For the fullest statement yet made of the habitats and years of appearance of the 14 broods of the 17-year race and the 7 broods of the 13-year race, see Bulletin 14, New Series, of the Division of Entomology, U. S. Department of Agriculture, 1898. As an example of the overlapping of the habitats of two broods of the same race, observe that, on pp. 48 and 49 of this Bulletin, three of the counties of Iowa and three of Missouri are given as part of the district where Brood XIII will appear in the year 1912, and also as part of the district where Brood XIV will appear in 1913, both broods being of the 17-year race. Broods XXI and XXII, of the 17-year race, are also reported as appearing a year apart in Wilkes County, North Carolina.

under some special influence of the environment upon members of the species that are geographically or locally isolated from the rest of the species.

But may not variation in the flowering season of a fairly homogeneous species 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 best adaptation to the environment? I believe that it not only may, but must have this effect; and that the result will be that the average form which flowers at the most favorable 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 isolation 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.

5. *Spatial Isolation.*

Spatial isolation is isolation arising from the relations in which the organism stands to space. I distinguish two forms, viz, geographical and local isolation.

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

Local isolation is isolation 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 isolation should be classed as geographical or local, still the distinction will be found useful, for the results will differ according as the isolation is chiefly due to barriers or to wide diffusion of the species. In geographical isolation 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 autonomic isolation.

Three different forms of spatial segregation may be distinguished according to the causes by which they are produced, viz:

Migrational isolation, caused by powers of locomotion in the organism.

Transportational isolation, 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.

Geological isolation, 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 can not 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 isolation 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 isolation has existed.

There is one important respect in which spatial isolation differs from all other forms of isolation, namely: In its ordinary operation it does not bring together those of similar endowments, and does not depend on diversity. 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 more or less liable to be affected by spatial isolation; and it often happens that other forms of isolation arise through the previous operation of this form; but as spatial isolation prevents organisms from crossing only when separated in space, it must always be reinforced by other forms of isolation before well-defined species are produced that are capable of occupying the same district without interbreeding. Many slightly divergent forms arising through local isolation are reintegrated with the surrounding forms, new divergences constantly coming in to take the place of the old; but if, during its period of local divergence, industrial or chronal isolation 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.

As spatial isolation does not necessarily depend upon diversity in the qualities and powers of the organism, it usually fails of distributing the varieties of a species 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 organisms 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 isolation between the different sections and of integration between the members of one section are, therefore, sufficiently clear; but what are the causes of differences of character in different sections, especially when they are exposed to the same environment? These causes all come under what I call typal intensification through diversity of success and diversity of survival.

6. *Fertilizational Isolation.*

Francis Galton's short article on "The Origin of Varieties," which was published in Nature, vol. XXXIV, p. 395, refers to this cause of isolation. 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.

It is evident that isolation of this form depends on divergence of character already clearly established, and, therefore, on some other form of isolation 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 isolation that precedes fertilizational isolation, producing the conditions on which it depends, must, in the majority of cases, be local isolation. Chronal and impregnational isolation, when imperfectly established, might be fortified by fertilizational isolation, but, in the case of plants, these are usually dependent on previous local isolation.

7. *Artificial Isolation.*

Artificial isolation is isolation arising from the relations in which the organism stands to the rational environment.

The importance of environal isolation.—We must not assume that the various forms of environal isolation 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 environal forms of isolation 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 isolations 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.

8. *Environal Partition.*

Environal partition depends on influences quite similar to those producing environal isolation, except that the seasonal, cyclical, and fertilizational forms are wanting. This is because these forms depend on inherited characters rather than on acquired habits, while environal partition is due to incompatibility in the acquired habits of individuals usually belonging to groups that have been locally separated for a time. Industrial and migrational partition tend more or less directly to produce groups with somewhat divergent habits, while transportational, geological, and artificial partition open the way for divergent forms of innovation, tradition, and election, to establish divergent types of habitudinal groups. Moreover, these forms of partition tend directly to produce isolation and consequently divergent racial groups.

II. THE REGRESSIVE MODE OF EACH SEGREGATIVE PRINCIPLE.

Regressive selection may be produced either by the cessation or by the reversal of a long-established form of selection. Near the end of the last chapter we referred to the Old World cuckoo and the American cow-bird as examples of degeneracy in the instincts for nest-building, for incubation, and for the feeding of their own young—a degeneracy that seems to have been produced by the gradual cessation of the selection by which these instincts had for countless generations been maintained. We also found that there was reason to believe that the discovery of substitutes for mother's milk is, in certain races of mankind, leading to decay of the power to give suck, through the survival of the children of mothers who, under the conditions of primitive times, would have entirely failed of having any share in the parentage of the next generation of parents. Examples of the reversal of selection are found in the history of species that, through the coming and going of the ice age, have for many generations been subjected to increasing cold, and then for many generations to increasing warmth.

Regressive election arises when any tradition or acquired character that has long been necessary for success in a given community ceases to be so. It often prepares the way for regressive selection. For certain races of dogs the traditional methods of finding food are very different from those that were current with their primitive ancestors, and the cessation of the necessity for the strenuous life of the old times has brought regressive selection, resulting in the decay of some of the old instincts.

What is usually called the amalgamation of races is *regressive isolation*. It is a form of racial demarcation, in which the boundaries are so changed that two or more slightly divergent varieties or races are interfused and become one. But, as I have already suggested, the limits within which regression of this kind can take place are comparatively small.

Regressive partition takes place when divergent forms of civilization become commingled and blended. In the case of human races it often introduces regressive isolation.

The most familiar of these four regressions is regressive isolation, that is, racial amalgamation, to which Darwin's work on *cross and self fertilization* has called attention. The chief significance of the principle lies in its producing a certain limited undoing of isolation and in its giving plasticity and variability to the compounded stock. Amalgamation usually arises through the entrance of divergent races into the same region before their sexual and social instincts or the physiological and structural coadaptations of the sexes have become so divergent as to prevent interfusion. Under such conditions whatever determines the bringing together of the races in the same region determines the nature of the amalgamation. When human races are brought together in the same region, the rapidity of amalgamation is determined largely by racial instincts and social conditions.

1. *Reversal of Partition and Isolation in Man.*

The most remarkable feature in the evolution of civilized man is the reversal of the processes of partition and of isolation and the breaking down of the social and racial segregations that have been progressing for countless generations. The leading factors in this process of coalition are social rather than racial; but the final result will undoubtedly be a great reduction of the number of races, and possibly a blending of all in one generalized type, resulting from the amalgamation of all the races in one. It is, however, possible that the barriers preventing marriage between certain races of men will become more fixed than ever, even though the intercourse of industrial, commercial, and national life becomes increasingly intimate. The era of commercial intercourse has been inaugurated and will never be reversed. Again, the smaller nations are being absorbed into the larger nations; but what the final result will be on the multitude of races and castes can not be easily foretold.

2 *Isolation Prevents Reflexive Selection between Groups.*

We are now prepared to understand one reason why isolation resulting from indiscriminate separation is in time transformed into segregation. *Isolation is in its very nature the suspension, not only of one form, but of all forms of reflexive selection between the separated portions of the species.* The importance of the cessation of natural selection in producing the different stages of the degeneration of organs that have ceased to be of use has been fully discussed by Romanes (see Nature, Vol. 41, p. 437, and previous communications there referred to), who points out that, as the power of the special form of heredity by which any organ has been produced has been built up by many generations of natural selection that have acted in favor of the organ, so the gradual weakening of that power follows the cessation of the natural selection. Professor Weismann seems to appeal to the same principle when he attributes the reduced size of "rudimentary organs" to the action of "panmixia." Now, since isolation always includes the complete cessation of reflexive selection between the separate groups, a similar principle is introduced, and the result must be the weakening of the power of heredity by which the portions of the species were held in correspondence with each other before their separation. I have elsewhere shown that isolation necessarily disturbs unstable adjustments; and we here see that the most stable of the adjustments by which each part of a species is kept in correspondence with every other part gradually becomes unstable, under the continued influence of isolation. Whenever a species is divided into two portions that do not interbreed, the forms of reflexive selection above described will cease to act between the two portions, and they will continue in sexual, social, physiological, and industrial harmony with each other only in so far as the force of the old heredity holds them to the old standards. But the force of heredity in these respects will in time fail if the reflexive selection that held the original stock in accord is entirely removed in its action between the two portions. If the separate breeding is long continued, incompatibility in all these respects tends gradually to arise; but it is manifest that incompatibility of industrial habits implies diversity in the forms of environal selection shaping each portion. I therefore maintain that separation, which necessarily includes the cessation of reflexive selection between the portions separated, is a cause of segregation and divergence and that it introduces diversity of environal selection, which is a still further cause of divergence.

III. DISCRIMINATE AND INDISCRIMINATE ACTION OF THE SEGREGATIVE PRINCIPLES.*

1. *Discriminate Action.*

Under each of these four segregative principles we may raise the question as to the difference in the results; first, when the principle under consideration is guided by some discriminative influence, continued from generation to generation, and, second, when it acts without discrimination and without cumulative results in successive generations. It is evident that *discriminative survival,* which is the same as selection, when continued in the same form for successive generations, must be cumulative in its effects. *Discriminative isolation,* that is, segregate intergeneration, arises whenever adaptation for appropriating certain resources brings together in one isolated group those that are by innate qualities and aptitudes the better adapted. In most of these cases it is not possible that another group should arise within this first group simply through being more highly endowed in the same respect. Cumulative isolation is for the most part produced by the subdivision of groups that have already been established, and the agencies producing the successive divisions are likely to be different in their nature, and, therefore, not cumulative in their effects upon any one character. This, however, does not prevent each isolation from being more or less segregative in regard to some of the characters.

Election, that is, the *discriminate success* of individuals through the attainment of certain habitudes and acquired characters, is likely to be cumulative in the effects produced on successive generations; for, as long as increased facility in the performance of certain acts is an advantage, both habitudes and aptitudes aiding in the performance will be combined in an increasing degree in each generation.

Discriminate partition, that is, segregate association, arises whenever adaptation for dealing with either the environment or the social conditions brings together in one separate group those that are by habitudes (that is, by acquired characters), the best adapted. It is manifest that among social organizations occasions producing such partition must often arise; and it seems probable that among even the least-endowed creatures great advantage must sometimes come to those who have in some degree acquired characters enabling them to meet new conditions in the environment, which come upon the species with a sweep that none who are unprepared can withstand. Such

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* See Table of "Discriminate and Indiscriminate Forms," page 136.

changes are sometimes experienced in temperature; or in the salinity of the water, in the case of water plants and animals.

2. *Indiscriminate Action of the Segregative Principles.*

Again, let us consider what the results are when the action of these principles is indiscriminate. *Indiscriminate survival* takes place in regard to any given character of a species when the presence or absence of the character has no effect on the adaptation of the individual. For Anglo-Saxons the possession of blue eyes or gray eyes is a matter of non-selective importance, and selection does not determine which shall prevail. There is, however, another form of indiscriminate survival which may have definite influence in determining the subsequent form of a race or species. I refer to the indiscriminate destruction of all but a small portion of the intergenerating group. Against heavy volcanic convulsions the varying endowments of different individuals of any one species usually count for nothing, and therefore the destruction falling upon them is indiscriminate; but if only a pair or two are left to propagate the species, the probability is that the type will be more or less changed in one or more of its characters.

Indiscriminate isolation of only a small fragment of a species is liable to result in important divergence in one or more of the characters of the species. If a single gravid individual, of a variable species of Hawaiian tree snails, is carried for a mile or two from its native valley while clinging to a leaf borne by a bird or a strong wind, it may fall in a neighboring valley, among groves and thickets of the same trees and shrubs that furnished its natural station in its original home. Is there now any probability that the colony descending from this individual, completely isolated from the original stock, but living in a valley with the same climate, and vegetation, and birds, and insects as are found surrounding their relatives in the original valley, will, by any chance, reproduce all the variations and varieties of the original species, and in the same proportions, and at the same time avoid producing any new varieties? My knowlege of variable animals in general, and my observations on Hawaiian snails in particular, make it impossible for me to believe that such a case could ever occur. If anyone says that an isolated portion of a species under absolutely the same environment as the original stock *must* produce the same varieties, as Wallace maintains in his volume entitled "Darwinism," I suspect he is using the word "environment" as equivalent for all the conditions that may cause divergence, whether they lie within the species or belong to what lies outside of the species. This seems to be in part the explanation of Wallace's position; for in enumerating the conditions in the environment that may have an effect in producing divergence, he calls attention to the fact that the small isolated portion of the species "is at once in a different position as regards its own kind." Now, this is exactly what I mean when I say that the isolation of a small portion has some effect in producing divergence, even if the conditions outside of the species could be absolutely the same as in the original habitat. Still further, as I have abundantly shown in the paper reproduced in Appendix II, it is very possible that the isolated portion will, early in its career, if not from the very first, be subjected to new forms of selection, through the adoption of habits of feeding that are wanting, or unusual, in the original habitat; for a rare habit in the original valley might become the predominant habit in the colony that arises in the newly occupied valley, even if the environments were *absolutely* the same. This form of selection I have called active (or endonomic) selection.

Indiscriminate success will arise in regard to any given habitude, or form of acquired efficiency, when the attainment or the non-attainment of the habitude has no effect on the success or influence of the individual. Another form of indiscriminate influence may be introduced by the indiscriminate slaughter of all but a few individuals of a community, in which case the habits of the few remaining individuals will have great influence on the habits of the new community arising through the multiplication of the few survivors.

Indiscriminate partition arises whenever the occasion that brings a number of individuals of a species together in a separate position does not determine that they shall be of any particular type of habitudes, of culture, or acquired skill. Partition due to an island being divided by partial submergence is usually indiscriminate; while migration often produces discriminate partition, as when it brings to a distant island men who are skilled in canoe building and sailing.

3. *Contrasts in Discriminate and Indiscriminate Forms of Action.*

These considerations bring to light the following facts:

(1) In the survival of innate characters and the success of acquired characters the discriminate forms (*i. e.*, selection and election) are of prime importance; for in one way or another they are continually acting on nearly every generation of nearly every species. The cases must be rare in which equal success and survival are attained by all the variations; for if variations in other respects have no effect, its variations in vigor will have relation to the degree of survival. In some rare cases there will occur the indiscriminate elimination of all but a very few members of a race or species; and the results

in such cases are liable to be of importance, through the original average character of the species not being fully represented and through the fact that this initial bias often leads to some new form of selection, which continues to act with cumulative force through subsequent generations. No single pair can exactly reproduce the average character of the species in all its aptitudes and habitudes, and therefore the methods of dealing with the environment adopted by the descendants are liable to be different.

(2) In isolation and partition there is less opportunity than in selection and election for cumulative effects in each generation. Moreover, in many of the cases, the isolation is indiscriminate till divergent forms of selection coöperate. But it should be noted that the isolation of a small number of the species is of frequent occurrence, and the failure of these small groups to represent the average character of the group or race either in habitudes or aptitudes introduces slight divergences determining new forms of autonomic selection which are of great importance in molding new types. And even when large masses are indiscriminately isolated all selection producing coördinations between the members of the separate groups ceases; and the probability is that in the course of many generations divergent forms of selection will arise, through different methods of coördination between members as well as through different methods of dealing with the environment adopted by different isolated groups. This probability rests not so much on the probability of a difference in the average character of the two large sections as on the probability that in one section some new habitude will arise that does not arise in the other section. The importance of isolation in producing divergence is seen not only in its being the absolute condition on which divergent forms of selection become of avail in producing divergence, but in the fact that the isolation of a few individuals often introduces from the first a divergent form of autonomic selection, though the environment is the same, and in the fact that the isolation of a large section of a species opens the way for a similar divergence of selection, though it may require many generations for the result to become apparent. Moreover, discriminate isolation (as when different industries have led individuals to form intergenerating groups according to their aptitudes), leads from the first to divergence in adaptations and to the intensification of adaptations.

The table on page 136 will be useful in enabling us to keep in mind the importance of these distinctions when applied to some of these principles. Discriminate survival, which is usually called selection, is of such importance that many terms have been needed to present the different influences through which it arises; while indiscriminate survival and it's equivalent, indiscriminate elimination, seem to be sufficient for the designation of a process which, as compared with selection, is rarely effective in producing the transformation of races.

4. *Table of the discriminate and indiscriminate forms of the four segregative principles.*

THE EIGHT FORMS.	THE RESULTS.
PARTITION.	
1. Discriminate partition = segregate association.	1. Grouping of individuals according to habitudes and acquired characters, and so producing habitudinal segregation, and giving an initial tendency toward segregate breeding.
2. Indiscriminate partition with more or less loss of power to perpetuate the original habitudes unchanged.	2. More or less divergence in the habitudes and acquired characters of the separated groups, especially when the groups are very small, and so producing initial habitudinal segregation.
SUCCESS.	
3. Discriminate success = election.	3. Success and influence of individuals according to their acquired fitness for the conditions, both social and physical, in which they are placed, producing intensified habitudinal segregation.
4. Indiscriminate success = indiscriminate failure.	4. When the number of individuals that escape from a sweeping catastrophe is very small, they will be unable to perpetuate the original social organization unchanged.
ISOLATION.	
5. Discriminate isolation = segregate intergeneration.	5. Grouping of individuals according to their aptitudes and innate characters, and so directly introducing segregate breeding with divergence of characters, *i. e.*, racial segregation.
6. Indiscriminate isolation with more or less loss of power to reproduce the complete average of the innate characters of the original stock.	6. More or less divergence in the aptitudes and innate characters of the isolated groups, especially when at the time of the first setting apart the group is represented by but one, or but few, individuals, and so producing initial racial segregation.
SURVIVAL.	
7. Discriminate survival = selection.	7. The efficiency of individuals in living and propagating will vary (and so their survival will vary) according to their innate fitness for the struggle of life, and thus the fitness of the race will be increased.
8. Indiscriminate survival = indiscriminate elimination.	8. When those indiscriminately surviving are very few, it will be impossible for them to reproduce all the innate characters of the original stock unchanged.

CHAPTER VIII.

CLASSIFICATION OF THE FORMS OF THE PRINCIPLES PRODUCING ALLOGAMIC EVOLUTION.

I. Tables of Forms, with Brief Explanations

The analysis presented in the two preceding chapters has revealed many factors, which are here brought together in tables so arranged as to show the more important of their relations to each other. (See pages 138–139.)

1. *Allogamic, Autogamic, and Agamic Evolution.*

A complete classification of the factors of organic evolution must include the principles producing differentiation of organisms multiplying asexually, as well as of those reproducing sexually. Moreover, the reproduction of self-fertilizing species is so unlike that of species in which cross-fertilization takes place (either in each generation or at the end of a series of generations), that it seems necessary to consider their methods of transformation separately. Following these distinctions, organic evolution needs to be divided into three departments, which may be called:

Allogamic evolution, which relates to the evolution of cross-fertilizing organisms;

Autogamic evolution,* which relates to the evolution of self-fertilizing organisms; and

Agamic evolution, which relates to the evolution of organisms whose reproduction is continuously asexual.

The investigation presented in this volume relates to allogamic evolution.

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* Karl Pearson, in 2nd ed. of "The Grammar of Science," London, 1900, p. 423, uses the term "Autogamic Mating" to designate self-fertilization.

2. *Allogamic Evolution Controlled by the Four Principles of Segregation.*

B. Habitudinal segregation ∵ autonomic association = I + III, and heteronomic association = V + VII, controlled by segregate association of individuals according to their acquired habitudes and resting on tradition and innovation, with habitudinal generalization and accommodation.

C. Typal demarcation ∵ autonomic demarcation = I + II, and ∵ heteronomic demarcation = V + VI.

(E) Habitudinal demarcation, through partition.

Coincident partition.

- *a.* Reflexive partition.
  - 1. Conjunctional partition.
    - (1) Family partition.
    - (2) Social partition.
  - 2. Institutional partition.
    - (3) Linguistic partition.
    - (4) Religious partition.
    - (5) Educational partition
    - (6) Sanitary partition.
- *b.* Environal partition.
  - 3. Endonomic partition.
    - (7) Industrial partition.
    - (8) Migrational partition.

I. Autonomic partition.

  - 4. Heteronomic partition.
    - (9) Transportational partition.*w*
    - (10) Geological partition.*w*
    - (11) Artificial partition.

V. Heteronomic partition.

- *c.* Regressive partition.
- *w.* Indiscriminate partition.

D. Typal intensification ∵ autonomic intensification = III + IV, and ∵ heteronomic intensification = VII + VIII.

(G) Habitudinal intensification through success (through election when discriminate).

Coincident election.

- *g.* Reflexive election.
  - 10. Conjunctional election.
    - (29) Sexual election.
    - (30) Social election.
    - (31) Filio-parental election.
  - 11. Dominational election.
  - 12. Institutional election.
    - (32) Religious election.
    - (33) Educational election.
    - (34) Sanitary election.
    - (35) Penal election.
- *h.* Environal election.
  - 13. Endonomic election.
    - (36) Habitudinal election.
    - (37) Aptitudinal election.

III. Autonomic election.

  - 14. Heteronomic election.
    - (38) Natural election.
    - (39) Artificial election.

VII. Heteronomic election.

- *i.* Regressive election.
- *y.* Indiscriminate failure.

A. Racial segregation ∵ autonomic intergeneration = II + IV, and heteronomic intergeneration = VI + VIII, controlled by segregate intergeneration of individuals according to their innate aptitudes and resting on heredity and variation, with racial generalization and adaptation.

(F) Racial demarcation through isolation.

Coincident isolation.

- *d.* Reflexive isolation.
  - 5. Conjunctional isolation.
    - (12) Sexual isolation.
    - (13) Social isolation.
  - 6. Impregnational isolation.
    - (14) Dimensional isolation.
    - (15) Structural isolation.
    - Physiological isolation
      - (16) Potential isolation.
      - (17) Segregate fecundity.
      - (18) Segregate vigor.
    - (19) Segregate adaptation
    - (20) Segregate freedom from competition.
    - (21) Segregate escape from enemies.
  - 7. Institutional isolation.
- *e.* Environal isolation.
  - 8. Endonomic isolation.
    - (22) Industrial isolation.
    - (23) Chronal isolation.
      - Seasonal isolation.
      - Cyclical isolation.
    - (24) Migrational isolation.

II. Autonomic isolation.

  - 9. Heteronomic isolation.
    - (25) Transportational isolation.*x*
    - (26) Geological isolation.*x*
    - (27) Fertilizational isolation.
    - (28) Artificial isolation.

VI. Heteronomic isolation.

- *f.* Regressive isolation.
- *x.* Indiscriminate isolation.

(H) Racial intensification through survival (through selection when discriminate).

Coincident (or organic) selection.

- *j.* Reflexive selection.
  - 15. Conjunctional selection.
    - (40) Sexual selection.
    - (41) Social selection.
    - (42) Filio-parental selection.
  - 16. Dominational selection.
    - (43) Sustentational domination.
    - (44) Protectional domination.
    - (45) Nidificational domination.
    - (46) Mating domination.
    - (47) Prepotential domination.
  - 17. Impregnational selection.
    - (48) Dimensional reflexive selection.
    - (49) Structural reflexive selection.
    - (50) Potential selection.
    - (51) Fecundal selection.
  - 18. Institutional selection.
    - (52) Ecclesiastical selection.
    - (53) Military selection.
    - (54) Sanitary selection.
    - (55) Penal selection.
  - 19. Prudential selection.
- *k.* Environal selection.
  - 20. Endonomic selection.
    - (56) Habitudinal selection
    - (57) Aptitudinal selection

IV. Autonomic selection.

  - 21. Heteronomic selection.
    - (58) Natural selection.
    - (59) Artificial selection.

VIII. Heteronomic selection.

- *l.* Regressive selection.
- *z.* Indiscriminate elimination.

3. *The Forms of Selection Defined.*

‡†*Organic* (or *Coincident*) *selection* is determined by accommodation that protects the group from extinction till coincident variations have time to arise.

j. Reflexive selection, based on relations within the group.

*†15. *Conjunctional selection,* ∵ coöperation of individuals especially ∵ the coördination of instincts and habits with qualities.

- (40) *Sexual selection* ∵ coördination of sexual instincts and qualities.
- (41) *Social selection* ∵ coördination of social instincts with qualities.
- *†(42) *Filio-parental selection* ∵ coördination between the powers and characters of the parents, and the size, number, form, and instincts of the young.

16. *Dominational selection* ∵ power to outdo, outrun, and overcome others of the same group in appropriating needed resources.

- (43) *Sustentational domination* ∵ taking food.
- (44) *Protectional domination* ∵ taking positions affording safety.
- (45) *Nidificational domination* ∵ taking positions for breeding.
- (46) *Mating domination* ∵ monopolizing mates.
- (47) *Prepotential domination* ∵ superior potency of pollen.

*17. *Impregnational selection* ∵ structural and physiological coördinations that secure a sufficiency of impregnated germs with least waste.

- (48) *Dimensional selection* ∵ coördination in length of pistils and pollen tubes, and in size of other impregnating organs.
- (49) *Structural selection* ∵ coördination of clasping organs, etc.
- (50) *Potential selection* ∵ coördination of the sexual elements.
- (51) *Fecundal selection* ∵ coördination in the relative number of the male and female elements preventing waste.

†18. *Institutional selection* ∵ suppression of reproduction for (52) Ecclesiastical, (53) Military, (54) Sanitary, and (55) Penal reasons; or the favoring of certain types.

†19. *Prudential selection* ∵ delay of marriage and prevention of reproduction for economic and other personal reasons.

k. Environal selection ∵ relations of the group and the environment.

20. *Endonomic selection,* determined by activities in the group.

- †(56) *Habitudinal selection,* determined by acquired habitudes.
- *(57) *Aptitudinal selection,* determined by innate aptitudes.

*‡IV. *Autonomic selection,* determined by the habitudes and aptitudes of each group.

‡21. *Heteronomic selection,* determined by activities in the environment.

- (58) *Natural selection,* determined by the irrational environment.
- (59) *Artificial selection,* determined by the rational environment.

‡VIII.

§*l. Regressive selection,* as when accommodation preserves those of inferior racial endowments.

Explanation of the signs used in Sections 2 and 3.

= Equal to. + Combined with.
∵ By means of; produced by; through.
* Determined by previously attained aptitudes.
† Determined by previously attained habitudes.
*† Determined by aptitudes and habitudes.
‡ Determined by conditions in the present environment.
§ Determined by one or more of these influences.

4. *Conditions Determining the Forms of Selection.*

The forms of selection depend on the following conditions (the letters and numbers are those used in the tables on pages 138–139):

j. The relations in which individuals of the same group stand to each other; that is, the *reflexive* conditions. First, the *aptitudes* (*i. e.*, instincts and other inherited powers), that shape these relations to each other; second, the *habitudes* (*i. e.*, habits and other acquired powers), that shape their relation to each other; and, third, the *physical characters* of the individuals, must be coördinated.

k. The relations in which the group stands to the environment, that is, the *environal* conditions (arising from the action and reaction between the group and its environment), must be harmonized.

20. The conditions within the group that shape these relations to the environment; that is, the *endonomic* conditions, being (56) the *habitudes*, and (57) the *aptitudes* that enable the isolated group to determine how it will use the environment, must be kept in the fullest possible accord with these uses and with each other.

21. *Heteronomic* conditions, (58) *natural* and (59) *artificial;* that is, conditions in the environment that constitute a limit to the possible methods of escape from destruction. Small colonies of Hawaiian snails, of the same species, isolated in neighboring valleys, but occupying the same species of trees and feeding in the same way, and all exposed to the same enemies, it seems to me are probably subject to the same forms of heteronomic environal selection. Any snail, capable of living on several species of trees growing in thick, shady groves, when brought to a valley where only one species of such trees is found, is subjected to *heteronomic* conditions, for but one method of survival is open to it. But even under these conditions we find divergence taking place in isolated groups. Shall we attribute such divergence to diversity of selection or to the diversity presented in the average character of the groups when first isolated? I believe this latter explanation is the more reasonable. If each colony was originated by a single snail, we know it is impossible that these original progenitors of the different colonies should in every respect have possessed the same characters. It is also impossible that the variations occurring in an isolated colony springing from a single pair should be exactly the same variations, presented in exactly the same proportions, as in the mother colony from which they were separated.

The influences determining the forms of isolation, partition, and election are also presented under the aspects of reflexive influences and environal influences, and in constructing terms for the different forms of these three principles we are able to avail ourselves of the adjectives that have been used in designating the different forms of selection. This is a great aid in presenting the relations between the four principles in their different forms.

In many of the places where the sign ∵ (meaning *caused by*) is used after the forms of reflexive selection, it might with equal correctness be changed to ∴ (meaning *causing*). For example, social selection may be described on the one hand as *depending* on the coördination of social instincts and qualities, and on the other hand as *building up and maintaining the social instincts and the characters on which they depend.* Taking a special case: Without any possible method of recognizing each other there could be no social selection; but, on the other hand, when a new race is formed, it is social selection that seizes on some new and fluctuating character, emphasizing, intensifying, and rendering it permanent; and so, in an important sense, it may be said that social selection produces the recognition marks and calls and coördinates them with the special instincts of the race that recognize these marks and respond to these calls.

II. AUTONOMIC AND HETERONOMIC INFLUENCES.

1. *Autonomic Influences Include Endonomic and Reflexive Influences.*

The nomenclature given in this volume calls attention to the fact that *endonomic selection* is determined by habitudes and aptitudes for dealing with the environment, and is subject to diversity without any corresponding diversity in the environment; and that the forms of *reflexive selection* are determined by the necessity for sexual, social, and other coördinations between the members of the same intergenerating group, also undergoing change without reference to change in the environment. The forms of endonomic and reflexive selection are, therefore, brought together under the term *autonomic selection*, which sets them in strong contrast with *heteronomic selection*, which is always determined by conditions in the environment surrounding the intergenerating group. But the effects of changes of activities within the intergenerating group, and not depending on changes in the environment, are not all covered by autonomic selection. We must also consider the autonomic forms of *isolation*, *election*, and *partition*, for they are all of importance in segregating and molding the types of allogamic organisms.

Autonomic isolation includes both endonomic isolation, produced by industrial, chronal, and migrational isolation, and reflexive isolation, produced by sexual and social instincts, by impregnational incompatibilities, and by institutional requirements. It is in contrast with *heteronomic isolation*, which is determined by conditions outside of the organic group, as, for example, geological subsidence, or causes resulting in transportation to an isolated position.

Autonomic selection coöperating with autonomic isolation produces *autonomic generation;* and heteronomic selection coöperating with heteronomic isolation produces *heteronomic generation.*

Autonomic election includes endonomic election, produced by the success of different acquired methods of dealing with the environment, and reflexive election, produced by the social promotion or suppression of individuals according to the success of their habits in relation to others of the same group. It is in contrast with *heteronomic election,* which is determined by conditions outside of the organic group.

Autonomic partition includes endonomic partition and reflexive partition, and secures the grouping of individuals as regards their habitudes, through the influence of activities that lie within each associating group. It is in contrast with *heteronomic partition,* which is the grouping of individuals as regards their habitudes, through the influence of activities in the environment.

Autonomic partition combining with autonomic election produces *autonomic association;* and heteronomic partition combining with heteronomic election produces *heteronomic association.*

Habitudinal intensification may arise from activities entirely within the group of organisms, of which social promotion and social suppression* of habitudes are familiar examples, and the combined effects of these activities on the habitudes of the group is appropriately called autonomic election; but we need a term to designate the combined influence of autonomic election and autonomic selection, producing the intensification of inherited aptitudes, in addition to the intensification of acquired habitudes. Such a term is *autonomic intensification.* It signifies the molding of types by activities within the intergenerating and associating group. In contrast with autonomic intensification, we have intensification produced by the combined action of heteronomic election and heteronomic selection, which may appropriately be called *heteronomic intensification.*

The coöperation of autonomic partition and autonomic isolation I call *autonomic demarcation;* and the coöperation of heteronomic partition and heteronomic isolation I call *heteronomic demarcation.*

The coöperation of autonomic intensification with autonomic demarcation produces *autonomic segregation;* and the coöperation of heteronomic intensification with heteronomic demarcation produces *heteronomic segregation.*

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* Baldwin defines *social suppression* as "Suppression of the socially unfittest by law, custom, etc." (See "Social and Ethical Interpretations," Appendix B.)

2. *Autonomic Partition Produces Autonomic Isolation.*

In the evolution of the European races of man the tendencies which break down ancient segregation, whether resting on habitudes or aptitudes, are so strong that it is difficult for us to apprehend the conditions of society in which segregative tendencies are in full force. The caste system of India not only maintains with absolute strictness the old barriers based on traditions received from remote generations, but tends to create new divisions, resting at first on industrial habits, but in time reinforced by separate social customs, separate ideals, and separate methods of training, and are finally intrenched behind restrictions forbidding marriage with those who were once considered as belonging to the same caste. Professor Reinsch states* that there are no less than 3,000 castes in India; and missionaries who have studied the institutions of the country most carefully assure us that if a caste is defined as an intermarrying group that is completely excluded from marriage with all other groups, then the castes of India number many thousands. Of the Brahmins, who are considered the highest caste of India, there are over 1,800 such sub-castes.

Rev. J. P. Jones, D. D., of Pasumalai, South India, informs me that during his residence in Southern India a branch of a certain barber caste has taken up the trade of weaving; and feeling that their occupation, which is being transmitted from father to son, sets them above the barber caste, they are now beginning to require that the son of a barber desiring to marry the daughter of a weaver must give up barbering and become a weaver.

The one remaining step required for the full establishing of the new caste will probably come within a few years, and will be the objecting to additions to the guild from those who have not been born within its ranks. Though railroads and other influences from Europe tend toward freer intercourse, these new castes are struggling into existence; and the tendency is to fortify the spirit of segregation by refusing to eat or have close fellowship with any outside of the caste that has thus recently come into being.

The caste system as developed in India is as unlike the democratic conservatism of China as it is opposed to the progressive individualism of European races. It may be doubted whether the caste system of India can ever develop into a truly progessive system. But the essentially democratic life of China stands in a very different relation to the progressive element of European civilization. In innate racial qualities no people can surpass the Chinese; and their vitality and power of adaptation is such that they seem to be equally fitted for suc-

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* See "The Forum" for June, 1901.

cess in all climates and in all countries. Moreover, under the stimulus of intercourse with European civilization, there are evident signs that new and progressive elements will be added to the old ideals till a truly progressive spirit is attained. *The remarkable power of accommodation to different climates and health conditions* possessed by the race, especially by the branch occupying the southern provinces of China, is such that few races are able to endure free competition with them even when the country and climate are so chosen as to give the best possible chance to their rivals. Members of the Teutonic race, when subjected to the climate of India, suffer from the effects of the heat; and their small power of individual adaptive modification in that direction gives them but little prospect of becoming completely adapted through the effects of natural selection; for, if their children remain continuously in the country, they have not sufficient energy for the battle of life. On the other hand, the Chinese from Canton, with high powers of accommodation, are fully successful as permanent settlers, both in the cold of Manchuria and in the heat of the Malay Peninsula, Borneo, and the Philippine Islands, and if completer racial adjustment is needed, they are sure to attain to it in the course of generations, through the accumulation of coincident variations.

In the last chapter of his Problems of Evolution, Headley discussed from a biological point of view some of the problems arising in the intercourse of eastern and western races.

III. An Unwarranted Assumption.

In discussing the influences producing evolution some writers have assumed that all diversity of survival in different groups of individuals of the same species is due to diversity in the environments to which the groups are exposed; and as natural selection is defined as the influence of the environment in determining what individuals shall survive, the inference is reached that diversity of natural selection is the only influence producing diversity of survival. A careful study, however, of causes producing diversity of survival in isolated groups shows that this assumption is without foundation. In the first place, it ignores the fact that diversity in sexual selection, and in any one of the other forms of reflexive selection, depends on diversity in the influence of members of the group upon each other, and that these influences may pass through a considerable range of divergence without change in the conditions lying outside of the species. In the case of man the forms of reflexive selection depend chiefly on the form of social organization, which may be subject to great change without reference to change in the environment of the group. In the second place, it ignores the fact that diversity of environal selection may be brought about either by diversity in the activities of the environment (that is by heteronomic selection), or by diversity in the organism determining its methods of dealing with the environment (that is, by endonomic selection).

Small differences may of course be found in the conditions presented in any two isolated positions; but when the divergence in the groups of organisms is not in accord with nor in proportion to these, it can not be attributed to them. If, however, we find that the form of selection is determined by the methods of using the environment adopted by the group, and that this is determined by the innate aptitudes of the individuals that founded the colony, I call the principle aptitudinal selection. If again, the method of using the environment, and so the form of selection, is determined by the training and acquired habits of those founding the group, I call the principle habitudinal selection.

Still further, there are strong reasons for believing that divergent forms of survival may arise in isolated groups, not only when the environment surrounding each group is the same, but when the habitudes and aptitudes of the individuals establishing the groups are the same. If we select two islands as completely alike in climate and resources as can be found, and plant upon the same two colonies of a few families each, selected in such a way that the average character of the colonies, in both innate and acquired characteristics, shall be as much alike as possible, and if we then subject them to complete isolation from each other and from the rest of the world, will they not in a few generations become divergent in language, in dress, in customs, in industries, and, if the experiment is continued through scores of generations, even in race characters? This might be called spontaneous diversity of election in partitioned groups, producing divergence of habitudes, and finally divergence of habitudinal selection, and so divergence in race characters.

In Professor Conn's Methods of Evolution, 1900, will be found a very lucid statement of the importance of isolation as a primal factor in all divergent evolution; but his plan of exposition aims at giving in broad outlines the main factors, rather than a complete analysis of the influences producing each.

CHAPTER IX.

SUMMARY AND CONCLUSION.

I. SUMMARY.

1. *Segregation.*

As segregate breeding is the fundamental principle producing racial segregations, and as isolation and selection coöperate in controlling the degrees and forms of segregate breeding, and therefore in controlling variation and heredity, so also it will be found that segregate association is the fundamental principle producing habitudinal segregation, and so partition and election coöperate in controlling the forms of segregate association, and therefore in controlling innovation and tradition.

It is also evident that the initial racial segregation introduced by discriminate isolation, or by the indiscriminate isolation of a few pairs, may be greatly hastened and intensified by the exposure of the isolated groups to diverse forms of selection; and it is no less certain that, even when the environment is virtually the same, diverse forms of selection may be introduced by diverse methods of using the environment that are liable to be adopted by the isolated groups. Moreover, it is equally evident that the initial habitudinal segregation introduced by discriminate partition, or by the indiscriminate partition of a single pair, may be greatly hastened and intensified by the exposure of the separated groups to diverse forms of election arising from the various forms of success, which are determined by the activities that become habitual in each group.

The evolution of organic types is originated and maintained by partition and election producing habitudinal segregation, and by isolation and selection producing racial segregation. Without these principles producing their intensifying and ramifying effects on organic types, the complex world of life could never have arisen out of the simple forms of primitive life; and without the continuance of the segregations thus produced the diversity that has been reached would soon be dissolved and the whole world of life would be reduced to but one species. But the history of races and species shows, on the one hand, that segregate breeding when fully fortified by physiological and psychological incompatibilities is never removed; and, on the other hand, that whenever increasing stringency of segregate breeding is in any way introduced, there we have either the transformation of some existing species or the setting apart of new groups that grow into new species unless reabsorbed by crossing or exterminated by competition.

The whole process of bionomic evolution, whether progressive or retrogressive, whether increasingly ramified and divergent, or increasingly convergent through amalgamation, is a process by which the limitations of segregate breeding are either set up and established or cast down and obliterated. But, as we have already seen, on the side of amalgamation an impassable barrier is in time reached in the physiological and psychological incompatibilities of long-established types, while on the side of advancing segregation the possibilities are constantly increasing. The general result is that new isolations and incompatibilities are constantly arising, forming new races and species, which in time become so divergent that it is impossible for them to coalesce under any conditions.

2. *Unbalanced Propagation.*

If we wish to find a principle which, if continued from generation to generation, will steadily tend towards the transformation of type, it is unbalanced propagation continuously of the same sign. That is, if the result desired is increase of the character under consideration, the selection in successive generations must be of those individuals that possess the character in more than the average degree; and such selection may be said to be continuously of the plus form. If the individuals selected in each generation depart from the type, but are so selected that those above the average are exactly sufficient to balance those from below the average, the average character of the mixing mass will be the same as the average of the original stock; and again, if the selection is plus in one generation and equally minus in the next generation, the result will be uncertain, even though long continued, for the effects of selection in one generation will be balanced by the effects of selection in the next generation, and we shall have one form of balanced selection. With a definition of balanced propagation that includes balancing of both the kinds just mentioned, we may say with confidence that unbalanced propagation, if continuous, will produce transformation, and that balanced propagation of the type, if continuous, will produce stability of type, and that balanced propagation of forms, some of which are considerably above the type and others of which are considerably below the type, will produce fluctuating variation.

We may next ask, how is unbalanced propagation brought about? The answer is that, in both natural and artificial breeding, it may be brought about either by the unbalanced effects of the processes separating the individuals into coexistent groups that are prevented from intergenerating, or by the unbalanced effects of differing degrees of survival for different forms of variation. The former principle is called "isolation," and the latter principle "selection." It is quite evident that in as far as selection prevents any form from propagating, in so far it prevents intergeneration between that form and the forms that produce the next generation; but, at the same time, I prefer to define isolation as the prevention of free crossing between *coexisting* groups, though the individuals of each group, so far as they survive, are freely intergenerating. When pointing out the correspondences between selection and isolation, I would say that both are principles by which the abiding principle of segregate breeding is modified and intensified; and that when either of them produces unbalanced propagation effected by the same sign in successive generations, the result is transformation of type.

During the process of domestication the reproductive powers of many species are so impaired that it is with difficulty that a permanent domestic race can be produced. Many individuals that thrive on the nourishment furnished fail to leave offspring, so that the race is perpetuated not by the offspring of those which are most pleasing to those who keep and select them, but by the offspring of those which have offspring. The same principle may produce transformation in species that are not under domestication. For if, among the many varieties, there arises one that, while retaining equal adaptation, is more fruitful than other varieties, it will be favored by *fecundal selection.* The descendants of the most fertile will have the largest share in producing the next generation. This will tend to produce increasing fecundity in succeeding generations. This is a form of discriminate survival; but we must remember that this fecundal selection will produce accumulation of other characters besides fecundity only when fecundity is correlated with certain variations that do not represent the typical or average form; that is, only when it is unbalanced fecundity. This seems to be a necessary law. As a corollary from this law, I judge that, in a stable intergenerating species or variety, the average form will be found to be most fertile; or, at least, the forms that depart from the average will not be continuously endowed with higher fertility than the average form. In considering the effect of selective survival we have to discriminate between balanced and unbalanced selection. Unbalanced selection is either the selection of individuals above the average producing an increase of the character thus selected or the selection of individuals below the average producing a decrease of the character thus discriminated against. Balanced selection is usually secured by selecting individuals of the average form, and tends to produce increasing stability.

3. *Cumulative Effects through the Coöperation of Different Principles.*

Two or more of the factors mentioned in this volume may coöperate in rendering a type more stable, or in rendering its previously attained characters more intense, or in diminishing its present characteristics while others are brought into prominence. If the organisms under consideration form but one intergenerant, any transformation thus produced will be monotypic; but if through the coöperation of isolation they form several intergenerants, any subsequent transformation will result in polytypic evolution.

Again, if each factor working by itself would tend to produce the same result, the united influence of several factors working together will be much more decisive than that of but one of them working alone.

4. *Cumulative Effects through the Operation of the Same Principle in Successive Generations.*

Once more it should be noted that the effect of unbalanced selection when continued through many successive generations is vastly greater than when lasting but for one generation. Indeed, on reflection it becomes apparent that the great difference between selective survival and non-selective survival is that the former is continuous from generation to generation, while the latter is accidental, and, therefore, not continuous. Moreover, in non-selective survival the effects of survival in any one generation are liable to be in a measure neutralized by the effects of survival in succeeding generations. Discriminate isolation is more effective than indiscriminate isolation because it is more effective in bringing together in one group a considerable number of individuals that belong to the same class; that is, that are either of average character, or above the average, or below the average. Indiscriminate isolation is less likely to bring together a special type and to repeat the process through many generations, and is, therefore, usually less effective than discriminate isolation in producing transformation.

The probability that a cumulative result will be reached through the effects of indiscriminate isolation, dividing the whole species into two large and nearly equal groups, without the coöperation of selection or without the continuous and cumulative effects of suetude (*i. e.*, of use or disuse), is very small; but we must remember that when isolation has become effective in shutting out all individuals of other groups, divergent selection, divergent suetude, and different forms and degrees of amalgamation are liable to arise. This liability is enhanced in case the fragment indiscriminately separated is small; for there is then a possibility that, in some one of its habitudes or aptitudes, it will differ from the original stock in such a way as to insure its using the environment in a somewhat different manner. It is certain that isolation is a principle tending toward the introduction of diversity not only in the forms of environal selection affecting the species, but also in the forms of reflexive selection, of suetude, and of amalgamation.

The distinction indicated by discriminate and indiscriminate isolation pertains only to the generations when group-formation is being shaped by additions brought in from the parent stock or from other groups, and these are usually the earlier generations of the new groups; but the influence of this primal shaping will continue through subsequent generations.

The action of discriminate survival and of suetude is, however, not at all confined to the earlier stages of group formation.

5. *Amalgamation.*

After a group has been considerably differentiated, combination with other groups is described as amalgamation.

Amalgamation, or the crossing of races that have been segregated for many generations, is a most effective process for introducing variation; and, if the contrast is not too great, for adding vigor to the stock.

6. *Some of the Facts Emphasized in this Volume.*

(1) That segregation is the underlying principle throughout the whole process of bionomic evolution.

(2) That the causes producing and intensifying segregation are quite various, and can not all be included under the term "selection," and that in seeking the causes of organic evolution we must investigate all the natural causes modifying the action of segregate breeding.

(3) That some of the most powerful influences in the control of segregation are due not to different forms of activity in the environment, but to diversity of activities in the organism, and may, therefore, be classed as forms of autonomic segregation.

(4) That habitudinal demarcations, through partition, are the initial forms of grouping, which, when intensified by election, produce habitudinal segregations, and that habitudinal segregations are often the controlling factors leading to racial segregations.

(5) That in reflexive selection (that is, selection produced by the relations of members of a species to each other), the influence of the environment in producing the special result is usually very obscure,

though there can be no doubt that it is sometimes operative. Social organization is often affected by the conditions in the environment; but though the environment remains unchanged, vast changes in social organization may take place. For example, while remaining in the same region, and without special change in the environment, a tribe of men may pass from the hunter stage of life, through something of pastoral life, into agricultural and diversified industrial life. This has probably been the experience of the Chinese race.

(6) That endonomic selection, resting on the power of different individuals of the same species to deal with the same environment in different ways, is a fruitful cause of divergent evolution in isolated sections of the same species. This diversity of power is sometimes due to diversity of aptitudes, producing what I call aptitudinal selection; and sometimes to diversity of training and of habitudes, producing what I call habitudinal selection; and at still other times to different methods of using the same aptitudes and habitudes, for which a suitable name has not yet been suggested.

(7) That organic (or coincident) selection is of great importance in securing a new adjustment when the organism is suddenly exposed to an environment very different from that to which it was previously adjusted.

(8) That the indiscriminate isolation of a small fragment of a species leads directly to the modification of type in the descendants of the isolated fragment, for the character of a single individual (or even the average character of several individuals) seldom if ever represents the average character of the original stock in every respect.

(9) That indiscriminate isolation of a large section of a species interrupts the unifying influences of tradition and of heredity between separated branches of the original stock; and, even though the environment surrounding each branch is the same, the traditional method of dealing with the environment may in one or in both branches become modified, and the separate branches be thus subjected to divergent forms of endonomic selection.

(10) That the indiscriminate elimination of all but a small fragment of an intergenerating group may be an important factor in introducing transformation, for one or two individuals may not be able to transmit all the traditions of the original group, or to reproduce in the innate characters of their offspring the unchanged average character of the original stock.

(11) That advancing powers of accommodation, coöperating with higher degrees of altruistic social organization, are in an ever-increasing measure setting aside both environal and dominational selection, and so lowering the racial standards of civilized man.

(12) That a perverted form of prudential selection is threatening the very existence of some nations that are counted highly civilized.

(13) That the only remedy for these destructive tendencies lies in enlightened and renovated institutional and prudential selection, and the wide adoption of higher ideals.

(14) That the most marked characteristic of modern human history is found in the breaking down of many of the minor segregations, both social and racial, of previous eras, and the ever-increasing intercourse between nations and races.

(15) That, notwithstanding the general trend of the new era, among the millions of India many new castes have been established during the past century.

II. CONCLUSION.

1. *What has been Gained by Recognizing Habitudinal Segregation?*

Having completed our study of the four principles of segregation, let us turn to the classification given in Appendices I and II, and consider *what has been gained by the distinct recognition of habitudinal segregation.* In Appendix I the combined action of partition and election, producing segregate association of individuals according to their acquired characters, and of isolation and selection, producing segregate intergeneration of individuals according to their innate characters, is presented under the single term "segregation." The action and reaction between the two spheres of segregation is not clearly presented, and, under the nomenclature there given, it would be difficult to consider all the aspects in which this interaction is manifested. In Appendix II, assimilational, stimulational, suetudinal, and emotional intension are used to designate intensification, produced by the different forms of accommodation and of acquired characters; while other terms are used to designate the intensification produced by the different forms of unbalanced propagation, securing the survival of certain types of variation in innate characters. The interaction, however, between habitudes and aptitudes is not as clearly presented in these earlier papers as in the chapters of this volume.

2. *A Method of Study that should be fully Applied.*

I believe the facts of distribution to which I call attention are of great importance, and that the methods of collecting and of exhibiting by which these facts have been brought to light is worthy of being applied in other fields. This method may be regarded as a development of the study of "centers of creation," initiated by Louis Agassiz and transformed by Darwin, Wallace, and others into the study of geographical distribution as affected by migration and divergent evolution. In order to perfect the method it is important that the creatures under study should be labeled at the time of collection with the conditions (of feeding, etc.) under which each specimen was found, and should be exhibited on maps setting forth as fully as possible the conditions presented by the environment at each point. An important step in this direction has been made by the late Professor Hyatt, of the Museum of the Boston Society of Natural History, in constructing a model of the island of Oahu, on which the geographical relations of the species and varieties of snails from that district may be exhibited. It would, however, be a great gain if a model (or at least a map) of the island of sufficient size were so arranged as to allow the shells themselves to be placed upon it in their true positions, instead of being represented by letters and numbers. The advantage of both methods might be attained by having, in addition to the model of the island arranged according to Professor Hyatt's method, a very large map on which the shells might be placed.

The method might be further improved by the use of colors and other devices for indicating the species of plant on which each specimen was found. The influence of temperature, humidity, and other external conditions, and especially of the conditions interfering with free crossing, may also be studied by exhibiting the average character attained under different stages of the influence and the degree of segregation resulting from the full action of the combined influences.

The degrees of segregation that have taken place in the inhabitants of a series of districts presenting different degrees of geographical isolation may also be studied by the determination of place-modes by statistical methods. Information on the mathematical methods that have been applied to this and other allied problems in biology will be found in the works of Francis Galton, Karl Pearson, C. B. Davenport, and others, and in "Biometrika," a journal for the statistical study of biological problems.

3. *The Study of Conditions Favoring Segregation.*

A rich field for the study of organisms under conditions favoring segregation will be found in the fauna and flora of island groups. The most interesting conditions will appear where the majority of the species are able to distribute themselves with some degree of freedom from island to island, while some one organic form is unable to pass the water barriers, except on very rare occasions. In such a region *we shall, I believe, always find a series of nearly related varieties or species distributed in the midst of a comparatively uniform environment.* Similar results will undoubtedly be found *wherever a group of organisms* *that is variable but of very limited powers of migration has been for many generations surrounded by a mass of species possessing ordinary powers of variability and ordinary facilities for distributing themselves.*

If this prediction is found to be in accordance with facts, it will show that the explanation of divergent evolution to which we have been led by the investigations presented in the foregoing chapters is essentially correct.

4. *Prediction Confirmed by Partula of Tahiti.*

Since writing the preceding statement, I have read with the greatest interest Dr. A. G. Mayer's memoir on "Some Species of Partula from Tahiti; A Study in Variation." The conditions of variation and migration which he brings to light in the case of some of the snails of Tahiti are a fine example of the conditions which I have found in the Hawaiian snails to be most favorable for the segregation of many closely related forms within a comparatively limited district, each section of which presents essentially the same environment. These conditions are, in the case of the closely related but divergent forms, a full degree of variability, but a very limited power of migration, and in the surrounding species the ordinary endowments in regard to variation and migration. *Partula hyalina* is found in all the valleys of the island of Tahiti; also on the Austral islands and on one of the Cook group. It may, therefore, have opportunities for migration that are not possessed by the other species of Partula found on Tahiti; and certainly it does not present the tendency to variation in form and color which we find in some of these species.

Of these other types I will refer only to three species which are found in four valleys, in which the character of the vegetation is essentially the same. On the north side of the island are three approximately parallel valleys, Piræ, Fautaua, and Tipærui. The first and last of these are about 3 miles apart, Piræ lying on the east and Tipærui on the west, while Fautaua and several narrow gorges lie between them. These three valleys are, however, "broad and well-watered, and contain a luxuriant growth of wild plantains and Caladium, upon which the snails are found in large numbers." Besides *Partula hyalina*, mentioned above as found in all the valleys of the island, there are two species of Partula found in these valleys. *Partula filosa* is found only in Piræ, and though constantly dextral presents divers shades of color. *Partula otaheitana* is found in all three of the valleys, but presents hereditary tendencies differing in each of the valleys; for example, in Piræ it is constantly sinistral, in Tipærui it is constantly dextral, and in Fautaua dextral and sinistral forms are found in nearly equal numbers.

On the south side of the island, about 27 miles from the three valleys just mentioned, is the valley of Vaihiria, where *Partula sinistrorsa* is found. This species, though closely related to the two species last mentioned, has adopted a different habit of feeding. "The Caladium and the wild plantain grow here in abundance, but most of the snails were found upon the wild turmeric, almost none being discovered upon the Caladium, and but few upon the leaves of the wild plantain." It is very variable in color, but easily distinguished from those of similar color in the valleys first mentioned by its lack of a tooth on the body whorl, by its relatively thin and fragile lip, by its more constricted suture, and by the lack of variation in the color of the young. Of its individuals 90 per cent are sinistral and 10 per cent dextral.

From these facts Doctor Mayer draws the following conclusions:

> *Partula hyalina* is very stable in all of the valleys, and gives rise to no varieties. All the other species, however, are remarkably variable, and give rise to numerous color-sports. These color-sports tend to breed true to themselves, and, therefore, to originate new color-forms and finally new species. This tendency is, however, held in check by frequent inter-crossing with the parent stock, and becomes effective only when the new color variety is isolated, or when it displays a remarkably strong tendency to breed true. * * * It is probable that geographical isolation plays a most important part in the formation of new species. If two valleys be adjacent, their snails are closely related each to each, whereas the wider the separation between any two valleys the more distant the relationship between their snails. The ridges between the valleys, being either barren or covered with vegetation unsuitable to the snails, afford barriers over which the animals must find it more or less difficult to pass. Thus the Partulæ in the Tahitian valleys are isolated very much as are the Achatinellidæ of Oahu in the Hawaiian Islands. * * * As far as the very limited observation of the writer goes, there appears to be no difference in the character of the snails in different parts of the same valley. The difference between any two adjacent valleys is, however, very marked.

The full statement of these facts and conclusions will be found in Memoirs of the Museum of Comparative Zoölogy at Harvard College, Vol. XXVI, No. 2, published in 1902.

5. *The Power of the Organism to Control its Relations to the Environment Increases with the Stage of Evolution Attained.*

We have shown by direct observation that it frequently happens that the same species of snails, when distributed in isolated groups in districts furnishing the same environment, establishes divergent methods of dealing with the environment, and so determines the form of selection to which it is subjected in the different districts. Moreover, this *power of the organism to control its relations to the environment* is found to belong in a higher degree to vertebrate animals, and especially to birds and mammals, while immeasurably the highest power of thus shaping his relations belongs to man. Civilized man not only changes his relations to the environment, but by agriculture and other arts transforms the environment to suit his own needs. In all its action inorganic matter is completely indifferent to the character of the results, either within the mass that is acting or in things external to it; but organic life is, throughout all its grades, striving to attain an increasing power of race preservation under given conditions, and, in its highest manifestation in man, it breaks largely away from the ancient thraldom, and assumes an ever-increasing control of the environment.

6. *The Chief Method of Advance is Tentative Variation with Transmission to Offspring of the Endowments of the Survivors.*

Throughout this whole struggle for ascendency *the principal method of advance* is the sending forth of various tentative experiments in the form of variously endowed individuals presenting many methods of dealing with the environment, each individual that survives having some influence on the endowments of the next generation. This law of the survival of the fittest applies to all from the lowest to the highest; but the qualities that constitute fitness differ progressively. In one stage, strength and such weapons as teeth and claws are of the greatest importance; in another stage, the degree of intelligence and the power to produce artificial weapons is the test; and, in a still higher stage, the power of social organization and the ethical ideals that form the foundation for such organization become the supreme necessity for survival. But throughout it is the same law of survival, the survival of the fittest, the future continuance of those fitted to continue. Though plants are without conscious purpose, we necessarily regard their production of flowers and seed as anticipatory action; for the whole significance of the process is found in its helping to secure continued propagation.

To an observer at the equator, the sun rises and sets each twenty-four hours, moving in a circle nearly perpendicular to the horizon, while to an observer at the North Pole the sun would rise and set but once in a year, and in each twenty-four hours would move through a complete circle nearly parallel to the horizon, traveling, as conventional language would say, from left to right; and to an observer at the South Pole, the same sun would rise and set but once in a year, and would circle in the reverse direction, that is, from right to left. Now, in such a case as this, we do not say that the cosmic process is changed. So also, in the case of ethical man, I would not say, as Huxley does, that his life is in opposition to the cosmic process, but rather that he has attained to one of the higher stages of that process, in which the meek are the ones who inherit the earth.

7. *Accommodation, Coöperation, and Anticipation.*

There are three spheres in which it is evident that progressive adaptation for beneficent action may take place, commencing with the smallest beginnings in the lowest organisms and progressing through each higher stage of evolution till the widest reaches are attained.

These three spheres are *accommodational action* (whether tentative or directly discriminative), *coöperative action*, and *anticipatory action.* Power for action in these spheres is characteristic of the realm of life, and is manifested in higher and higher efficiency till accommodation tries to prove all things, holding fast that which is good; and coöperation, associated with division of labor and community of interest, reaches out to include in its beneficence the living universe; and anticipation, pressing forward in its unbounded aspirations and ideals, becomes the ever-advancing influence of foresight and prediction in the activities of the highest beings.

8. *Increasing Recognition of Autonomic Factors.*

It will be observed that throughout the whole process of evolution there are two classes of factors, of which one class may be called heteronomic, in that they are subject to change through change in activities lying outside of the group of organisms concerned, while the other class may be called autonomic, in that they are controlled by changes within the group of organisms. In the theory of evolution presented by Darwin, the importance of the heteronomic factors was emphasized, though he pointed out one form of autonomic transformation, which he designated by the term "sexual selection." To some expounders of evolution natural selection has seemed so completely sufficient that they have been ready to deny the influence of sexual selection (or of any other autonomic factor) in producing divergence. On the whole, however, there has been during the past ten or fifteen years an increasing recognition of the fact that not only sexual selection but other autonomic factors are more or less effective in controlling the forms of selection, and, therefore, in controlling the transformations of organisms. Do we not thus reach one explanation of the continuous advance—the determinate evolution—of certain large classes of animals?

The recognition of autonomic factors in the process of evolution is giving new insight into the self-developing endowments of the organic world.

APPENDIX I.

REFLEXIVE SEGREGATION.*

[A small portion of "Divergent Evolution through Cumulative 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 between members of the group in all the circle of relations in which the organism stands; but, in order to insure isolation 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 obstructed or prevented and isolation 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.

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* Under "Demarcational Segregation" I class the influences by which organisms are distributed in separate groups. It includes both environal segregation and reflexive segregation, and is equivalent to isolation as now generally used. In the section of this paper on Environal Segregation (not here reproduced), I considered the forms of isolation arising from the relations of the species to the environment. A classified table of the forms of segregation will be found near the end of this paper.

† Read December 15, 1887. From the Linnean Society's Journal, Zoölogy, Vol XX.

10. *Social Segregation Produced by 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 subdivision. 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 group 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, often holding apart groups but very slightly differentiated; while in the case of many animals the sexual instincts of the males tend to break up these minor groups. Though the barriers raised by social instincts are often broken over, their influence is not wholly overcome, and in many instances 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 coöperates 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 vigor 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 selection 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 crossing within the same

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* Numerals are used to designate causes of segregation not depending on human purpose. Of these nine were mentioned in the section on environal segregation.

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 somehow 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 favor 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-accumulated 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 distinct characteristics 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 the seeds produced by each individual plant shall be fertilized by the pollen of the same 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, of the Ovules of a Flower by Pollen from the same Flower.*

Some 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 does not fail of propagating in England, though Darwin found that it was very rarely visited by insects that were capable of carrying the pollen, and the pollen is not carried by the wind.* Darwin also mentions *Ophrys apifera* as an orchid which "has almost certainly been propagated in a state of nature for thousands of generations without having been once intercrossed."†

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

† *Ibid.*, p. 439

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 favored by self-fertilization occasionally interrupted by interbreeding with individuals of another stock; for the latter is favorable as introducing vigor and variation, and the former as giving opportunity for the accumulation of variations.

These two methods of propagation are so far removed from those found in the majority of species that it may be wise to consider any transformation arising under such conditions as belonging to a separate department of the process of evolution. Organisms that are self-fertilized in all their generations seem to stand in nearer relation to species entirely without the power of sexual propagation than to species in which cross-fertilization is the usual method of propagation.

(*b*) IMPREGNATIONAL SEGREGATION.

Impregnational segregation is due to the different relations in which the descendants of one original stock stand to each other in regard to the possibility of their producing fertile, vigorous, and fully adapted offspring when they consort together.

In order that impregnational segregation should be established and perpetuated, it is necessary, first, that variation should arise, from which it results that those of one kind are capable of producing vigorous, adapted, and fertile offspring in greater numbers when breeding with each other than when breeding with other kinds; second, that mutually compatible forms should be so brought together as to insure 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 action of the different forms of impregnational segregation I call *negative segregation,* for they rest on incompatibilities interfering with mixed unions or allowing of no offspring, or of but few or inferior offspring, as the result of mixed unions, and, unaided by positive segregation, can do nothing toward bringing creatures together according to their compatibilities. The forms of segregation that place or draw together creatures of like innate characters I call forms of *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 complete lack of capacity for fruitful crossing is the cause that prevents the production of mongrels, we find a dependence of a very different kind; for to insure the propagation of the different groups it is not enough that the general opportunity for the members of the species 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.

The form of impregnational segregation which I call prepotential segregation is due to the prepotency of the pollen of a species or variety on the stigma of the same species or variety, and complete potential segregation is due to the potency of the pollen of the same species, with 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, aided by the free distribution of the pollen by the wind,* 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 diœcious 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, the probability is that 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. *When aided by this free distribution* the combined effect is that of positive as well as negative segregation; for the free distribution of the fertilizing element, with the superior affinity of the two sexual elements that are mutually prepotent, secures the interbreeding of the species or variety producing the mutually prepotent elements.

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 when once complete the groups affected never coalesce. 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 dimensional segregation, structural segregation, potential segregation, segregate fecundity, segregate vigor, segregate adaptation, segregate freedom from competition, and segregate escape from enemies.

14. *Dimensional Segregation (or Segregative Size) is caused by Incompatibility in Size or Dimensions of the Individuals of the Different Breeds.*

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. *Structural Segregation (or Segregative Structure) is Caused by Lack of Correlation in the 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, according as the male is of the one variety or of the other.

Segregative 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 freely cross 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 men.

16. *Potential Segregation (or Segregative Potency) in its Two Forms, Complete Potential Segregation and Prepotential Segregation.*

(1) *Nature of the Principle.*—It is caused by the greater rapidity and efficiency with which the sexual elements of the same species, race, or individual combine. Complete 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 reach the same ovum at the same time, or sometimes when the prepotent element comes many hours after the other. That propagation may result compatible elements must meet.

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 complete 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 principle is fundamentally one, though it will be convenient to retain both names.

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.

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

Some of these questions are as follows:

(2) *Points needing investigation.*—First. Are there many cases of prepotential as well as of complete potential segregation between different forms of water animals?

Second. Is prepotential segregation always accompanied by segregate fecundity and segregate vigor?

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

Fourth. 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. 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 than 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 Chapter XVI of "Variation under Domestication" it is suggested that prepotency of this kind might be a cause of different varieties of double hollyhocks reproducing themselves truly when growing in one bed, though there was another cause to which the freedom from crossing in this case has 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.*

(3) *Reasons for believing that potential segregation can not be accumulated by natural selection.*—Concerning this last point I wish to give reasons for a different opinion. I believe that qualities simply producing segregation can never be accumulated by natural selection, for—

First. 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.

Second. 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.

Third. When any segregate form begins to arise we can not attribute its success to the advantage of isolation, for it is not the success, but the separateness of the success, that is due to the isolation.

Fourth. 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 advantage of segregation over intergeneration is not 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.

(4) *How shall we explain the accumulation of potential segregation?*—But if the accumulation of prepotential segregation is not due to natural selection, how shall we explain it? The divergence of a group can not take place without its being segregated from the original stock as well as from other types; and the potency of the sexual elements of the new group will be maintained in their relations to each other by some form of reflexive selection; but as there can be no reflexive selection between the segregated groups, the potency of the elements for crossing outside of the group will in time be impaired; and then we

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

shall have prepotency of each group within the circle of its own group. This process may take place when a group is protected by complete isolation, however produced. Let us next consider a case in which a small group partially protected from mixture with the original type by incomplete local and industrial segregation produces a variation whose ovules are more readily fertilized by pollen from the same group than by pollen from the original type. Is it not evident that this variation will gain with each generation an increasing prominence in the new group that maintains somewhat new methods of dealing with the environment in its partially isolated habitat? This will be so, first, because variations possessing but little or no prepotency with their own group will eventually coalesce with the original stock, and especially will this be the case if the new group becomes somewhat numerous and passes beyond the limits of its narrow habitat into districts where the original type abounds; and, second, because variations possessing the prepotency with their own group in a superior degree will remain distinct, breeding with each other, and their descendants will become still more segregate and still more permanently divergent. Of *the law of accumulation of segregative endowments*, 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 will, however, soon be shown that unless the reproduction and power of survival is greater for the pure segregate forms than for the mixed forms, the proportion of pure forms to mixed forms will decrease in each generation.

It is evident that when either segregate potency or segregate prepotency is associated with the free distribution of the fertilizing element by wind or water, the combined effect must be in the former case complete, and in the latter case partial, positive segregation, for the breeding together of compatible forms is thereby secured.

It may at first appear that a slight degree of segregate 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 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 vigor, which we know are sometimes characteristics of varieties in their relation to each other.

17, 18. *Segregate Fecundity and Segregate Vigor.*

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 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 vigor 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 vigor are the terms by which I indicate the relation to each other of forms in which the highest fertility and vigor are produced by crossing, and not by independent generation.

19. *Segregate Adaptation.**

Segregate adaptation is the relation in which species or varieties stand to each other when the intergeneration of individuals of the same species or variety produces offspring better adapted than the

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* This and the following paragraph were not in the paper as first published, though the advantage of escape from severe competition with members of the same species was set forth in the paragraph entitled "Competitive disruption."

offspring produced by crossing with other species or varieties. Natural selection is the survival of the best adapted of the variations that remain and breed with the stock under consideration, but it takes no cognizance of the fitness or lack of fitness of individuals or a race that separate themselves from the intergenerating mass. The different grades of fitness for their new life found among the individuals that form the new intergenerating group will be the ground for divergent natural selection in the new group; but they will not affect the type of the original stock. Now, whenever the conditions and aptitudes of the two groups are so different that the offspring of cross-unions are less fitted for life under either set of conditions than is either group of the pure-breeds for its own peculiar life, we shall have a new principle, different in its effects from natural selection. This I call segregate adaptation. Natural selection is the survival of the fittest that intergenerate; segregate adaptation is the superior fitness and survival of the offspring produced by segregate generation.

20, 21. *Segregate Freedom from Competition and Segregate Escape from Enemies.*

Segregative endowments may be necessary to the enjoyment of certain advantages which are gained not by superior adaptation to the environment, but by endowments that set them in a position where competitors and enemies are as yet few. These two principles I have called segregate freedom from competition and segregate escape from enemies. *Segregate freedom from competition* or segregate access to unused resources results when the pure offspring have freer access to unused resources than do the cross-breeds or the original stock. *Segregate escape from enemies* (an advantage often of equal importance with that just mentioned) arises whenever the pure offspring of a divergent variety are able to occupy a position freer from enemies than that occupied by the original stock.

(*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 to be enumerated are national, linguistic, caste, penal, sanitary, and educational segregation.*

CONCLUDING REMARKS.

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

The negative forms of segregation would tend to produce extinction if they were not associated with the positive forms of segregation. But 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 potential segregation, and potential segregation coöperating with this free distribution results in positive segregation. 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 some degree of 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; and, 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

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* This completes the classification of the forms of isolation which are here presented as forms of demarcational segregation. It is probably correct to say that with the exception of transportational and geological isolation, and perhaps some cases of migrational isolation, all the forms of isolation so far discovered are, from the first, more or less discriminative, and, therefore, segregative. Moreover, if transportational or geological action plants an isolated colony of only a few individuals, the average type of the original stock is not fully represented in the colony and, therefore, the effect is more or less segregative from the beginning.

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* vigor and fecundity is the relation in which the varieties of one species often 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 vigor 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 vigor 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 seem to show that segregate fecundity and vigor 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 vigor 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 can not, 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 vigor 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 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.

2. *Isolation Usually Somewhat Discriminate, and therefore Segregative, from the First.*

Of the twenty-one natural forms of isolation enumerated in this paper, there are only two that are usually indiscriminate in their action. These are transportational segregation and geological segregation. And even these sometimes become discriminate in their action through the fact that those individuals that are similarly endowed are liable to be transported in the same way and to the same place, or to escape together from destruction in geological disturbances. Again, it may happen that by gradual subsidence a large island will be divided into two smaller islands, and thus certain species inhabiting the original island may be indiscriminately isolated. But even in such a case, unless the average inheritable character of each section of the species is exactly the same in all respects, the effect is segregative from the first. If one, or both, of the sections is very small, the probability of exact similarity in all respects entirely disappears, unless the species is wanting in plasticity and variability.

3. *Principles Intensifying Segregation.*

Besides artificial and institutional segregation, which depend on the rational purpose of man, we have now considered 21 forms of segregation, resting on purely natural causes.

At some other time I shall endeavor to present the natural laws that coöperate in intensifying the effects produced by the segregative causes already considered. Segregation is not simply the independent generation of different sections of a species, but the independent generation of sections that differ. Though indiscriminate isolation of a small section of a species may produce an initial difference, 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, and may be classed as a form of intensive segregation.

It has been observed that some of the causes enumerated in this 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 coöperate in securing a given division of a species, and one form is superimposed upon another, the aggregate effect must be 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 isolation whether in its separative or segregative forms. But the discussion of intensive segregation must be reserved for another occasion.

*A Lack in this First Classification of Segregative Principles.**

The classification of segregative principles here given does not draw any clear distinction between those resting upon acquired characters and habitudes and those resting upon innate characters and aptitudes. For example, industrial segregation is defined as "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." Now it is manifest that in some cases the different methods of using the environment may be determined by acquired habitudes rather than by inherited aptitudes, and the demarcation thus produced will, in the first place, be habitudinal, though in the end it may result in racial demarcation.

The interaction between the principles producing racial segregation and those producing habitudinal segregation is discussed in Chapter V (pp. 45–78).

It should also be noted that since this paper was brought before the Linnean Society, isolation has come into general use for designating the prevention of free crossing, by which the demarcation of racial groups is determined. This leaves the term "segregation" more free to designate the combined action of the principles producing the demarcation of groups and of those producing the intensification of the characters of the separated groups. Partition and isolation produce habitudinal and racial demarcation, while election and selection produce habitudinal and racial intensification, and the combined action of the four principles produces segregation both racial and habitudinal. (For a fuller statement see Chapters V and VI.)

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*As this explanation does not occur in the original paper it is printed in different form.

4. *Classified Table of Forms of Segregation.**

DEMARCATIONAL SEGREGATION [OR ISOLATION].

A. Environal segregation:		
(*a*) Industrial segregation.		
Sustentational		1
Defensive		2
Nidificational		3
(*b*) Chronal segregation.		
Cyclical		4
Seasonal		5
(*c*) Spatial segregation.		
Geographical Local	Migrational	6
	Transportational	7
	Geological	8
(*d*) Fertilizational segregation		9
(*e*) Artificial segregation.		
B. Reflexive segregation:		
(*a*) Conjunctional segregation:		
Social		10
Sexual		11
Germinal		12
Floral		13
(*b*) Impregnational segregation:		
Segregative size		14
Segregative structure		15
Potential segregation		16
Segregate fecundity		17
Segregate vigor		18
Segregate adaptation		19
Segregate freedom from competition		20
Segregate escape from enemies		21
(*c*) Institutional segregation.		

INTENSIVE SEGREGATION.

(*a*) Assimilational intension.
(*b*) Stimulational intension.
(*c*) Suetudinal intension.
(*d*) Emotional intension.
(*e*) Amalgamational intension.
(*f*) Selectional intension.
(*g*) Fecundal intension.
(*h*) Eliminational intension.

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*Numerals are attached to the forms of segregation found in natural species.

5. *Computation of the Effects of Different Degrees of Positive Segregation Coöperating with Different Degrees of Segregate Survival.*

Of the tables which are herewith presented Table I is an arithmetical computation, showing the number of half-breeds as contrasted with the pure-breeds, when nine-tenths of each variety form unions among themselves and double with each generation, while the offspring of the one-tenth that form mixed unions simply equal the number of the parents by which they are produced; in other words when $c = 0.1$, $M = 2$, $m = 1$ (see Table II).

TABLE I.

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 1.8	Initial number	...	...	1,000
1,800 = A (1.8) 1.8	1st generation.	100	...	1,800
3,240 = A $(1.8)^2$ 1.8	2d generation.	260	20	3,240
5,832 = A $(1.8)^3$	3d generation.	532	72	5,832
357.05 = $(1.8)^{10}$ computed by log. ∴ 357,050 = A $(1.8)^{10}$	10th generation	35,688	...	357,050
39,347.272 = $(1.8)^{18}$ ∴ 39,347,272 = A $(1.8)^{18}$	18th generation	3,934,725	...	39,347,272

EXPLANATION OF TABLE I.

The 2d generation of the half-breeds is found by taking nine-tenths of the previous half-breeds, *i. e.*, $100 \times 0.9 = 90$, and one-tenth of the previous pure-breeds (the one-tenth that form mixed unions), minus one-tenth of the previous half-breeds (because one-tenth 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 2d 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 one-tenth 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.

Table II is a preliminary formula for showing the proportion of half-breeds to pure-breeds.

Let $R = 1 - c =$ the ratio of pure breeding, *i. e.*, the segregation.

Let $c =$ the ratio of cross-breeding, *i. e.*, the segregation viewed from the other side.

Ex.—When nine-tenths of the unions are within the limits of the species and one-tenth of the unions are with an allied species $R = 0.9$, $c = 0.1$. 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.

TABLE II.

Number of individuals representing the pure form.	Number of individuals representing the half-breeds.
A = Initial number.	
$A(RM)$ = 1st generation.	1st generation = Acm.
$A(RM)^2$ = 2d generation.	2d generation = $(AcmR + A(RM)c - Acmc) \times m$.
$A(RM)^3$ = 3d generation.	2d generation = $(AcmR - Acmc)m + Acm(RM)$.
$A(RM)^4$ = 4th generation.	2d generation = $Acm(R - c)m + Acm(RM)$.
Substituting $(1 - c)$ for R in the 2d generation, we have $A(M - Mc)^2$ = 2d generation.	Substituting in this $(1 - c)$ for R, we have 2d generation = $Acm(1 - 2c)m + Acm(M - Mc)$.

EXPLANATION OF TABLE II.

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 2d generation.

TABLE III.—*Developed Formula for Positive 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 $= Amc.$
$A(M - Mc)^2$ = 2d generation..	2d generation $= Amc\ (1 - 2c)m + Acm(M - Mc).$
$A(M - Mc)^3$ = 3d generation..	3d generation $= Amc((1 - 2c)m)^2 + Acm(M - Mc)(1 - 2c)m + Acm(M - Mc)^2.$
$A(M - Mc)^4$ = 4th generation.	4th generation $= Amc((1 - 2c)m)^3 + Acm(M - Mc)((1 - 2c)m)^2 + Acm(M - Mc)^2(1 - 2c)m + Acm(M - Mc)^3.$*
	4th generation $= Amc(M - Mc)^3\left(\frac{((1 - 2c)m)^3}{(M - Mc)^3} + \frac{((1 - 2c)m^2}{(M - Mc)^2} + \frac{(1 - 2c)m}{(M - Mc)} + \frac{(M - Mc)^3}{(M - Mc)^3}\right).$
$A(M - Mc)^n$ = nth generation.	nth generation $= Amc(M - Mc)^{n-1} \times \Big(\big(\quad\big)^{n-1} + \big(\quad\big) + \big(\quad\big)^3 + \big(\quad\big)^2 + \left(\frac{1 - 2c)m}{M - Mc}\right)^1 + 1\Big).$

First 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.

Second 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 $1 + \frac{(1 - 2c)m}{M - Mc} + .$ containing as many terms as that expressed by the number of the generation, *i. e.*, containing n terms, of which the first is 1; $\therefore \frac{H}{P} = \frac{mc}{M - Mc}\Sigma\left(1 + \frac{(1 - 2c)m}{M - Mc} + \qquad\right)$; H being the number of half-breeds, and P being the number of pure-breeds.

Third Rule.—Without any change in this formula, we may use M and m, as suggested where we introduce Table IV, and thus find the combined result produced by the five forms of segregate survival, when coöperating with given ratios of positive segregation.

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* Dividing each term by $Amc\ (M - Mc)^3$ and then multiplying the whole by the same amount set outside of brackets, we have the next form.

Method of using Table III (see p. 179).

By supposing n to be an indefinitely high number, and by giving different values to M, m, and c, we shall have 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 there is not integrate fecundity, that is, 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 $S = \frac{a}{1-r}$, in which a is the first number of the progression, which in this case is 1, and r is the ratio of progression, which in this case is $\frac{(1-2c)m}{M-Mc}$ the fraction we are now considering. Supposing $c = \frac{1}{10}$, the fraction will be

$$\frac{\left\{1-\frac{2}{10}\right\}1}{1-\frac{1}{10}} = \frac{8}{9} = r; \therefore\ S = \frac{a}{1-r} \text{ becomes } S = \frac{1}{1-\frac{8}{9}} = \frac{9}{9-8}$$

$= 9$. 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 high number. Substituting these values in the last formula of the table, 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 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 degree of segregate survival, can not prevent a species being finally fused with other species. The pure-breeds must decrease as long as the whole number of each successive generation of pure-breeds does not increase by a multiple equal to or larger than $\frac{1}{1-c}$. That is, if $m = M$, and $M < \frac{1}{1-c}$ fusion will in time become complete.

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 from Table III, we shall find that the sum of the infinite progression is $\frac{9}{5} = \frac{18}{10}$. And $M - Mc = \frac{18}{10}$, which makes the half-breeds = the pure forms × cm; and $cm = \frac{1}{10}$. Let $M = 2$, $m = 1$, $c = \frac{1}{100}$; then half-breeds = pure forms × $\frac{1}{100}$. 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 × $\frac{1}{2}$.

TABLE IV.—*Simplified Formulas for the Proportions in which Half-breeds stand to Pure-breeds when all forms of Segregate Survival are considered.*

In each formula M may represent the ratio of those coming to maturity in each generation of the pure-breeds, and m may represent the ratio of success or failure of the cross-breeds in coming to maturity in each generation.

From Table III we learn that

$$\frac{H}{P} = \frac{mc}{M - Mc} \times \left\{ 1 + \frac{(1 - 2c)m}{M - Mc} + \left\{ \frac{1 - 2c)m}{M - Mc} \right\}^2 + \left\{ \quad \right\}^3 + \left\{ \quad \right\} + \right\}.$$

When $(1 - 2c)m$ 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 $S = \frac{a}{1 - r}$. Applying this formula we have

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

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

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

$$H = P \times \frac{mc}{M - m + (2m - M)c} \text{ . . . . Formula (2)}$$

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 × $\frac{3}{4}$.
$c = \frac{1}{3}$, half-breeds = pure-breeds × $\frac{3}{5}$.
$c = \frac{1}{4}$, half-breeds = pure-breeds × $\frac{3}{6}$.
$c = \frac{1}{5}$, half-breeds = pure-breeds × $\frac{3}{7}$.
$c = \frac{1}{6}$, half-breeds = pure-breeds × $\frac{3}{8}$.

TABLE V.—*From Formula* (2).

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

OBSERVATIONS ON TABLE V.

This mathematical analysis of the effects of positive segregation and segregate fecundity when coöperating brings distinctly into view several important relations.

First. Incomplete forms of positive 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.

Second. 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 positive segregation is intense, differences in the degree of segregate fecundity produce greater contrasts than the same differences do when the positive segregation is slight.

Third. 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 is as 1 to 100. This shows that when segregate fecundity is strongly developed, differences in the degrees of positive segregation produce greater contrasts than the same differences produce when the segregate fecundity is but slightly developed.

APPENDIX II.

INTENSIVE SEGREGATION, OR DIVERGENCE THROUGH INDEPENDENT TRANSFORMATION.*

I. CLASSIFICATION OF THE FORMS OF INTENSIVE SEGREGATION.

In a previous paper on divergent evolution I have enumerated many classes of natural causes which produce either separate or segregate generation,† and which, in their combined action, tend to produce cumulative segregation and divergent evolution in every part of the organic world. I have there shown, with sufficient fulness, that cumulative segregation always produces cumulative divergence or polytypic evolution; but I have not fully shown how separation from the first involves more or less segregation, or how segregation, which at first divides the species into sections with reference to some one endowment, is always tending toward intensified segregation in which the sections present differences in regard to an increasing number of endowments.

After expounding the principles on which these laws of divergence rest, I will give a few examples of divergence, calling attention to the complete correspondence between the facts of nature and the principles expounded in this and the previous paper.

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* From the Linnean Society's Journal, Zoölogy, vol. XXIII. Read December 19, 1889.

† Separate generation, or separation, is the indiscriminate division of a species into sections that do not intergenerate. Segregate generation or segregation is the independent generation of different sections of a species when the sections are composed of somewhat divergent classes of variations. Isolation differs from selection in that the latter denotes the exclusion of certain kinds from opportunity to propagate, while the former denotes the division of those that propagate into classes that are prevented from intergenerating. Isolation, or the prevention of intergeneration, whether it be through separation or segregation, I also call independent generation. Darwin used isolation as equivalent to geographical separation, while later writers have come to use it as equivalent to independent generation.

1. *Separation always Involves more or less Segregation, for no two Portions of a Species Possess exactly the Same Average Character.*

When a homogenous species is divided into two large sections, it may be difficult to prove by measurement that there is any difference in their average character; but on general principles we may assume that, at least in some points, there is a slight difference. It is evident that when the separated sections are small there is more likely to be *diversity* in the average character of the sections and that, roughly stated, the probability of divergence from this cause will be in direct proportion to the variableness of the species and in inverse proportion to the size of the different sections. When a few stragglers form a small colony in an isolated position there is the strongest reason to expect that they will not be able to propagate the characters of the species in exactly the same proportions in which they are produced by the main body of the species, or by any other small colony that is propagating independently; and when the original stock has been rendered highly variable by the crossing of somewhat divergent varieties, the degree of difference that will probably be presented by any two independent colonies will be correspondingly increased. *We must bear in mind that while specimens possessing an average character in any one respect are always abundant, those perfectly representing the average in every respect are rarely, if ever, found.* Now, is it to be supposed that any one or any small number of these imperfect representatives of a species will, if separated from the rest, transmit all the characteristics of that species in the exact proportions presented by the average character of the original stock?

Mr. Francis Galton has conclusively shown* that in the children of parents whose heights deviate from the average of the race to which they belong, there will be a similar deviation amounting on the average to a certain fixed proportion of that presented by what he calls the mid-parentage. The mid-filial deviation in the groups investigated by him was about two-thirds of the mid-parental deviation. There is, therefore, a regression in the average character of the offspring toward the typical character of the group. It must be observed, however, that this law can hold in full force only when there has been free crossing, for otherwise there will be no type from which the deviation can be measured.

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* See "Types and Their Inheritance," an address before the Section of Anthropology of the British Association in 1885; also "Natural Inheritance," p. 97.

2. *Eight Forms of Monotypic Evolution*

Let us now consider how this initial segregation, which is always present in the case of a small colony, is enhanced and intensified by the coöperation of other principles, and how forms segregated through possessing different characters in some one respect come to diverge in other respects. For example, when differences of color become the occasion for sexual and social segregation, how does this open the way for divergent transformation in habits of feeding and in a thousand other respects? The principles coöperating with independent generation in producing this enhanced divergence are all causes of simple transformation, or monotypic evolution when there is free intergeneration. Divergent breeds of domestic animals have always been produced when the different sections of a species in the care of different races of men have been prevented from interbreeding, thus securing their independent transformation during the process of domestication. So in nature, when any form of independent generation has been established, any cause of transformation that may afterwards arise will always produce more or less divergent evolution, and never that which is in every respect parallel. But we must defer the discussion of this subject till we have enumerated the more manifest of the principles of monotypic evolution:

(1) *Assimilational transformation*, or modification due to deficiency with economy, or redundance with profusion, of growth, resulting from different degrees of assimilative power. "Economy of growth" is a term already in use, but a term is needed that shall include both this and its opposite.

(2) *Stimulational transformation*, or modification produced by changed motions in the fluids of the organism responsive to changed influences in the environment. Under this principle we may place the direct influences of light, heat, electricity, the dampness of the air or the saltness of the water in which the organism is bathed, the quality of the food, and all stimulation from physical and chemical causes, exclusive of those resulting in muscular activity or the movement of the organs.

(3) *Suetudinal transformation*, or modification due to the effects of use, disuse, and habitual effort in producing motions, and in resisting the strain of gravity and other forces tending to produce motion. *Suetude* is not found in the dictionary, but I venture to use it as including *assuetude*, which is being accustomed to, being practiced in, habitual use; and *desuetude*, which is disuse, discontinuance of practice.

(4) *Emotional transformation.*—Dr. C. V. Riley, late of the National Museum, Washington, has called attention to the influence of parental emotions (especially maternal emotions during the term of pregnancy) as a factor in evolution (Address "On the Causes of Variation," before the Section of Biology, American Association, August, 1888; also in Popular Science Monthly, vol. XXXLV, pp. 811–816).

(5) The cumulative development of adaptations through "the survival of the fittest" when the fittest are other than average forms. This is the principle of *unbalanced selection* producing *selectional transformation.*

(6) Transformation produced by the indiscriminate destruction of a portion of a species, with the accompanying probability that the remaining portion will not possess all the characters possessed by the species previous to the elimination. This principle I call "*unbalanced indiscriminate elimination,*" producing *indiscriminate eliminational transformation.*

(7) Transformation produced by different degrees of amalgamation of the varieties and races which have resulted from previous segregations. In most species there is a constant process of amalgamation by which thousands of minor varieties are absorbed; but when the process extends beyond ordinary limits, and the barriers that have divided well-marked races give way, transformation must follow. This principle I call *diversity of amalgamation* producing *amalgamational transformation.*

(8) The cumulative development of the more fertile of the forms that are equally adapted. In other words, transformation produced by diversity in the relative fertility of varieties that are equally adapted to the environment and the constitution of the species, or by change in the degrees of fertility possessed by the same variety at different times and in different places. This principle I call *unbalanced fecundity,* or *unbalanced fecundal selection,* producing *fecundal transformation.*

Of these principles all except the sixth, seventh, and eighth have been more or less discussed by writers on biology, though some of the forms of selection depending on the relations in which the members of a species stand to each other have never been pointed out, and many writers have failed to observe that selection often produces fixity of type instead of transformation, and that divergence can not be produced through diversity in the kinds of selection without the coöperation of isolation, and may be produced without exposure to different environments.

Assimilational, stimulational, suetudinal, and emotional transformation belong to a class of factors producing what are known as acquired characters.*

Selectional, eliminational, amalgamational, and fecundal transformation may be classed as principles of unbalanced propagation. The principles of unbalanced propagation are abundantly established as genuine methods of change in the average inheritable characters of species, not only by experience derived from the domestication of plants and animals, but by observation of similar effects produced by natural processes.

3. *Principles of Vital Action not here Discussed.*

I have not mentioned "acceleration and retardation" as principles of transformation, for they seem to be but phases of the law of suetude; for, as explained by Cope, use or effort in the parents produces in the offspring accelerated inheritance, while disuse or cessation from effort produces in the offspring retarded inheritance.† So also Hyatt's "Law of Concentration" (or "acceleration," as he often calls it) seems to be a general law of inheritance relating to the transmission of characters originating under any and every principle, the effects, whether progressive or retrogressive, being inherited at earlier and earlier ages in each successive generation.‡ It is also doubtful whether correlated transformation should be considered a separate principle, for it seems to be simply the inheritance by offspring of characters that have for generations been united in the endowments

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*These four factors are included under what Prof. J. M. Baldwin calls accommodation (see Nature, April 15, 1897, also "Development and Evolution," pp. 94 and 151). *Accommodation produces three classes of effects:* (1) *Habitual activity (that is, repeated imitative and intelligent activities, aiding in self-preservation, or in the preservation of offspring or of the communal group);* (2) *modification (that is, acquired physiological and anatomical effects of activity);* (3) *active (or endonomic) selection determined by the habitual activities of the group in dealing with the environment.* For a description of accommodation in lower organisms see Contributions to the Study of the Behavior of Lower Organisms, published by the Carnegie Institution, 1904, where Herbert S. Jennings has shown in a series of elaborate experiments with Amœba, with ciliate infusoria, and with flagellates, that their usual method of response to any given stimulus is in accord with what Lloyd Morgan has called "The method of trial and error." This method I would describe as varied tentative action with repeated response till success is gained either by avoiding damage or by attaining advantage.

† "Origin of the Fittest," pp. 203–207, 228.

‡ Proceedings of the American Association, vol. XXXII, pp 352–361.

of at least a portion of their ancestry, and the correlation of these endowments must have been produced through the action of other principles.

The prevalence of males in times of pressure, with the prevalence of females in times of plenty, is regarded by Dr. W. K. Brooks, of Johns Hopkins University, as a characteristic established by natural selection, by which the organism acquires variability or fixity of type according as either character is most needed; for according to his observations the males represent the former and the females the latter element. There can be no doubt that in many species the males are more variable than the females, and that in some of the same species the proportion of males increases with the degree of adversity; but this does not seem to be sufficient ground for maintaining that the increase in the proportion of males will increase the variability of the offspring. Increase in the number or amount of the variable element does not necessarily involve increase in the variability of either element or in the offspring of both. I find need of additional factors in order to bring these facts into any relation to the increase of variability. Granting that the sperm-cell is the source of variation and the germ-cell the source of fixity, and that increased tendency to variation in the offspring will be secured by an increased range of variation in the sperm-cells, it does not follow that increase in the relative number of males will increase the range of variation in the sperm-cells, and, therefore, in the offspring. But if conflict in the environment and the winnowing process of natural selection falls most heavily upon the males, there must be some advantage in having their relative numbers increased in times of adversity; and if the exposure of parents to hardships increases the variability of either male or female offspring, and especially if it increases the variability of both, plasticity will be increased.

Professor Cope's "Doctrine of the Unspecialized" (Origin of the Fittest, pp. 232–235) rests on the fact that the most highly specialized types, as well as individuals, are most likely to be exterminated by extraordinary changes in the environment; and Mr. Hyatt's "Teratology" (Proceedings American Association, vol. XXXII, pp. 349–360) teaches that types that are being slowly exterminated usually assume forms resembling those produced by old age and disease in the individual. These and other laws in the growth and decay of types and individuals are of great interest, as they afford organic conditions under which the factors of transformation must act.

4. *The Transformation of Freely Intergenerating Organisms Never Permanently Divergent.*

I mention these eight principles of transformation, not with the purpose of entering upon a full discussion of the same, but simply to point out the relation in which they all stand to divergent, or polytypic, evolution. It is evident that, whether acting separately or together, they can never be the cause of divergent evolution in organisms that are freely intergenerating; for in such a group of organisms whatever modifies one part of the group in characters that are inheritable will, ere many generations, modify the whole. If the group is exposed to a variety of inharmonious conditions, which, with independent generation would produce divergent character, with free intergeneration, the only result will be variation. Without independent generation (or isolation) there can be no permanent divergence.

5. *Independent Transformation Always Divergent.*

If any species is divided into two or more sections that do not intergenerate and that are severally subject to highly complex transforming influences, it may only be by a series of coincidences which the reason refuses to receive as in the slightest degree probable that any two sections will be modified in exactly the same way. This high degree of probability, amounting to a certainty, that when causes of transformation coöperate with causes producing isolation the result in successive generations will be increasing degrees of segregation and of divergence, is what I call the law of *intensive segregation.* The different forms of this principle, resting on the certainty that the coöperation of any one of the principles of transformation with any one of the principles of independent generation will produce increasing segregation with increasing divergence, are the following:

(1) Assimilational intension, or segregation and divergence through independent assimilation.

(2) Stimulational intension, or segregation and divergence through independent stimulation.

(3) Suetudinal intension, or segregation and divergence through independent suetude.

(4) Emotional intension, or segregation and divergence through independent emotional transformation.

(5) Selectional intension, or segregation and divergence through independent selection.

(6) Eliminational intension, or segregation and divergence through independent and indiscriminate elimination.

(7) Amalgamational intension, or segregation and divergence through independent amalgamation.

(8) Fecundal intension, or segregation and divergence through independent fecundal transformation.

In groups that do not intergenerate, divergent forces reveal themselves whenever transformation is introduced. If it were possible to believe that the effects of independent selection or of independent suetude had been completely parallel, it would still be impossible to believe that both of these, together with the remaining six principles of transformation, would ever so combine as to produce completely parallel transformation in isolated sections of a species, even if all were surrounded by the same environment. This principle is not inconsistent with the introduction of what Professor Hyatt calls "representative of parallel characteristics" in two or more divergent series of forms. What he points out is that, under the influence of heredity, similar organisms exposed to similar environments undergo similar transformation (Anniversary Memoirs of the Boston Society of Natural History, 1880: "The Genesis of the Tertiary Species of Planorbis at Steinheim," pp. 24–29).

In the description of these principles I have used the adjective "independent" to signify that the principle is operating in sections of the species that are prevented from intergenerating. In the term "independent variation" Mr. Romanes has already used the adjective "independent" as meaning *"when accompanied with the prevention of intercrossing."*

6. *The Pervasive Influence of the Causes of Transformation and the Law of Intension.*

In my paper on "Divergent Evolution" I made the statement that "When separate generation is long continued we have reason to believe it always passes into segregate generation with divergent evolution." The same thought had been expressed in a previous paper by the statement that "Variation is so strong that all that is necessary to secure divergence of types is to prevent their intermingling."* The certainty that independent generation with transformation will never produce parallel, but always more or less divergent evolution is *the law of intensive segregation* already referred to. But in addition to this certainty there is a very strong probability that where independent generation is long continued, transformation of some kind will supervene. If there are any species in which the power of cumulative variation has

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* See "Diversity of Evolution under One Set of External Conditions." Journ. Linn. Soc., Zoöl., vol. XI, p. 499.

been entirely lost, this latter law can not hold in their case; but it is doubtful whether among species that reproduce sexually there are many such. The variability of some species is so small, and the conditions of the environment are so constant, that comparatively long periods of independent generation pass before perceptible transformation arises. This seems to be the case with the thirteen and seventeen year races of *Cicada septendecim*, to which I shall refer when giving examples from nature. From the high probability that long-continued independent generation (*i. e.*, isolation) will be followed by independent transformation, and the certainty that independent transformation will be divergent, there follows the corollary that long-continued independent generation will probably be attended by divergence. In other words, independent generation long continued is almost always attended by independent transformation; and independent transformation inevitably produces divergence. This double principle I call *the law of intension*. This law rests on the ubiquity of transforming influence and on the impossibility that in a species possessing any plasticity the inherited effects in any section independently generating should be exactly the same as in any other section. This is especially the case when the species is highly plastic and when the isolated section is very small.

We can not doubt that when a diversity of powers and susceptibilities in the different sections is acted upon by a great variety of influences the responses of the different sections will be unlike, and the result will be increasing segregation and increasing divergence. Now, it is impossible to doubt that in species propagating sexually and possessing some degree of plasticity, these are exactly the conditions whenever the species is divided into sections that do not intergenerate.

It should be observed that, in accordance with the principle of intension, not only is indiscriminate separate generation when long-continued transformed into more and more strongly segregate generation, but any form of segregate generation, resting on some one principle that causes the division of the species into sections differing in regard to some one form of endowment, will, if it is long continued, be inevitably reinforced and intensified by transformations, which, being independently combined and transmitted, will multiply the number of characteristics in regard to which divergence takes place. If, for example, the pollen of a given variety, when falling upon the stigma of the same variety or race, is prepotent over the pollen of every other variety or race that falls upon the same stigma at the same time, or at a somewhat earlier time, what I call prepotential segregation will divide the species into two groups that are prevented for the most part from intergenerating; and these separate groups, gradually coming under the influence of different degrees, forms, and combinations of the transforming principles, will in time become strongly characterized species. It is not, however, necessary that all or any of these forms of transformation should coöperate with segregation in order to produce a distinct species. The accumulated effects of segregation, unaided by these principles producing intensification, would be sufficient to produce well-defined species; but it is impossible that they should often remain unaided.

7. *Utilitarian and Non-Utilitarian Divergence.*

The principles of suetude and selection, though they are directly related to the development of utilitarian characters, may produce in the useful innate characters of isolated sections of the same species exposed to the same environment, divergence that is not necessary or advantageous; and the effects of the other six principles are often not only wanting in but opposed to utility. Assimilational transformation includes redundance of growth, which is not always, as well as economy of growth, which is always, utilitarian. Unbalanced elimination, amalgamation, and fecundity may be advantageous, useless, or disadvantageous. We have, therefore, in these six principles of transformation, abundant cause for the introduction of non-utilitarian characters; and, when accompanied by independent generation, they must be the source of multitudes of non-utilitarian divergences. In the earlier stages of divergent evolution the non-utilitarian distinctions are more abundant; for in the later stages multitudes of them are weeded out by economy of growth, as has been clearly pointed out by Mr. Romanes;* and still others through coming under new conditions in the environment or through some new habit of intelligence, become useful endowments, and are brought under the preserving and accumulating influence of natural selection or of suetude. It should, however, be noted that the development of useful specific differences is as much due to independent generation as is the development of useless specific differences. Diversity of suetude or of selection does not produce divergent evolution unless it coöperates with independent generation.

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* Physiological selection, Journ. Linn. Soc., Zoöl., vol. XIX, p. 383.

8. *Selectional Intension, or Segregation and Divergence Produced by Independent Selection.*

That we may gain a clear apprehension of the nature and influence of this principle, certain discriminations, which have not always been recognized by writers on the subject, are absolutely necessary; and, for the sake of avoiding misunderstandings, it is desirable that these distinctions should be represented by clearly defined terms. I am fully aware that many will be opposed to the introduction of new terms into the treatment of a subject that has been so long and ably discussed. If these discriminations were not found necessary by the author of the "Origin of Species," or if the distinctions, so far as recognized by himself and others, have been expressed in the language of ordinary description, why should a more accurate terminology be needed now? In reply it may be said that the freedom from technical language, which is a great advantage in a work which for the first time calls the attention of the world to a vast subject, is a serious defect when the exact relations of the subject come under discussion.

In order to secure clear thinking on the subject, I have found it necessary to keep the following distinctions constantly in mind:

(1) The selection that results in the transformation of species is not the selection of one species to the exclusion of another. The breeding of the horse to the exclusion of the ass modifies neither the one nor the other. It is the exclusive generation of certain variations of a single intergenerating group that gradually transforms the group. When, therefore, we speak of selection as a cause of transformation, we refer to the selection of the variations that are to interbreed and keep up the race, to the exclusion of other variations. In order to maintain the same distinction in the nomenclature of natural processes, what I call "*selection*" is caused by the failure of certain forms of a species to perpetuate their kind as contrasted with the success of other forms. If the failure includes all the forms of a species, I call it the *extinction* of that species and class it as a cause of transformation in the remaining species only so far as it makes a change in their environment.

(2) The exclusive generation of certain forms of an intergenerating group does not necessarily result in transformation. Experiments in artificial breeding show that if we select only the typical representatives of a race the general character of the race is not changed, though any tendency to fluctuating variation may be gradually diminished and the stability of the type increased. When, however, one form of deviation from the mean is constantly selected without a counterbalancing selection of the opposite deviation, the transformation of the

race is usually the result. In other words, *balanced selection produces stability of type, and unbalanced selection produces transformation of type.**

In the light of this twofold law we see how there may be stringent selection without transforming effect. In nearly every species there is a constant struggle between the different forms of variation; and as it never happens that all the forms are equally successful, the process of natural selection is always bearing in full force upon the species. If, then, it could be shown that natural selection, wherever it exists, must necessarily produce transformation, it would be impossible to resist the conclusion that nearly every species is undergoing transformation through this cause. But it is unbalanced rather than balanced selection that produces transformation. We also see that heredity tends to make the most successful form the average form, and thus to convert unbalanced into balanced selection. From this it follows that in order that selection should produce continuous transformation, covering a wide range, it is necessary that the form of variation selected should from time to time be changed. This may be expressed as the principle of *continuous transformation through successive changes in the character of the selection.*

Though selection produces transformation only when it involves the survival of other than typical forms, it is still very possible that there are only a few species in which completely balanced selection prevails for very many generations in succession. It is still certain that long-continued independent selection gradually passes into diversity of selection producing divergent evolution.

(3) Though in more than one passage Darwin maintains that uniformity of external conditions involves uniformity of natural selection, and that isolation can have no effect in transforming a species if physical conditions and surrounding organisms remain the same, still I think that if the question had been distinctly brought before him he would have admitted that exposure to a new or changed environment was not a necessary condition for change in the character of sexual selection. Now, I think it can be shown that, besides sexual selection, there are several forms of selection that depend upon the relations of the members of one species to each other and that may undergo change without the organism being exposed to a different environment.

Selection depending on the relations of the organism to the environment I call *environal selection*, of which I find two kinds, namely,

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* The general law is here stated, without any attempt to explain why selection, securing the exclusion of those falling below a certain standard, is necessary for the preservation of that standard in the case of many characters (see par. (6) below).

active and passive selection, and under passive selection I place natural and artificial selection. Selection depending on the relations of the members of a species to each other I call *reflexive selection*, the chief forms of which I call conjunctional, dominational, impregnational, and institutional selection.*

(4) It must be carefully noted that diversity of selection depending on diversity in the relations of the organism to the environment does not necessarily involve the exposure of the organism to different environments. In other words, change in even environal selection does not necessarily involve either change in the environment or the entrance of the species into a new district. Darwin's teaching seems, at times, to be in conflict with this statement, but there are passages in his writings which distinctly state that variations in instinct may lead to different habits of sustentation, and it is evident that this would naturally lead to a difference in the congenital qualities that win success in the different sections and so to difference in the environal selection.

It should be remembered, however, that the meaning of anyone's statements on this subject will depend on his definitions of the words used. What is meant by environment, external conditions, and other similar terms? Until we define we shall only beat the air, however exact our statements may seem to be. I therefore repeat what I have elsewhere stated, that, according to my definition, change in the environment is always change in activities that lie outside of the species, or of the segregated group, of individuals that is under consideration. In Darwin's usage the phrase "change in external conditions" seems to carry the same meaning; but in some cases this can hardly be the case.

Diversity in the uses to which isolated sections of one species put their powers, when appropriating resources from the same environment, must produce diversity in the forms of variation that are most successful in the different sections. This I call *active selection* as contrasted with *passive selection*, which varies according to differences in the environments.† All diversities of environal selection that do not vary according to differences in the environments must be classed as diversities of active selection, for they must have originated in some variation in the powers of the organism or in the diversity of uses to which it has put its powers. Diversity in the successful use of the powers of the species in dealing with the environment, whether

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* To these I now add prudential selection.

† For "active" and "passive" selection, I often substitute "endonomic" and "heteronomic" selection.

initiated by diversity in the action of the species in its different sections or by diversity in the nature of the different environments, necessarily introduces diversity of environal selection. This principle may be expressed as the *dependence of diversity of environal selection on diversity in the relations of the powers of the organism to conditions in the environment.*

(5) Diversity of innate powers in the different sections of a species can not be maintained and accumulated without some degree of segregation between the different sections, for within one intergenerating group every initial divergence is speedily merged in the general character of the group. This law may be briefly defined as the *dependence of increasing divergence of racial characters on the continuance of isolation.* As was shown in my paper on "Divergent Evolution," without the aid of causes preventing intercrossing, the selection of other than average forms will produce *transformation* but never *divergence*—will produce *monotypic* but never *polytypic evolution.*

(6) Diversity in the character of the selection may be introduced, not only by the intervention of new forms, but also by the cessation of old forms of selection. We shall find that important differences of this kind may arise, resulting in considerable transformation before any new form of selection has come into action. A good illustration of the *cessation of selection* is found in the increasing frequency with which human mothers, notwithstanding their failure to give suck, succeed in raising their children. The power to give suck is through this process being diminished in the more civilized races, though there is no reason to believe that those who do not give suck have, on the whole, any advantage over those who do. The new result is, therefore, being produced not by the introduction of a new form of filio-parental selection, but by the cessation, or the weakening, of the old form. Romanes has pointed out the effects that must often be produced by the cessation of natural selection,* but he has not considered the cessation of other forms of selection. In subsequent paragraphs of this section relating to social and filio-parental selection are given a number of examples of the influence of accommodation in causing certain forms of selection to cease and in certain cases introducing new forms of selection that are the reverse of the older forms.

(7) It is often convenient to distinguish between selection resulting from rational devices and that resulting from the superior success of

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* See an article on "The Factors of Organic Evolution," in Nature, vol. XXXVI, pp. 402–404, in which reference is made to previous papers in which the cessation of natural selection is discussed.

organisms better adapted than their rivals of the same intergenerant to the natural laws and conditions of the environment, or to the natural constitution of the species to which they belong. The former I call *rational selection* and the latter *adaptational selection.* Under the former I place artificial [prudential] and institutional selection, and under the latter I place processes as unlike as natural selection and sexual selection. This classification does not, however, seem to me so important or so fundamental and clearly definable as that which rests on the fact that some forms of selection depend on the relations in which organisms stand to the environment, while others depend on the relations in which the members of the same species stand to each other. It may here be noted that artificial selection is the exclusive generation of those that are better fitted to the rational environment, through the failure to propagate of those that are less fitted. The effect is the same whether the failure to propagate is through lack of adaptation to human purposes or through lack of adaptation to the unreasoning environment.

The following table of the *forms of selection* will, I think, be a help in maintaining these and other distinctions.

FORMS OF SELECTION.

		ADAPTATIONAL SELECTION.		RATIONAL SELECTION.
ENVIRONAL SELECTION.	Balanced and unbalanced.	*Active (or endonomic) selection.* Habitudinal selection. Aptitudinal selection. *Passive or heteronomic selection.* Natural selection.	Balanced and unbalanced.	*Heteronomic selection.* Artificial selection. Conscious. Unconscious.
REFLEXIVE SELECTION.	Balanced and unbalanced.	*Conjunctional selection.* Sexual selection. Social selection. Filio-parental selection. *Dominational selection.* Prepotential domination. Sustentational domination. Protectional domination. Nidificational domination. Nuptial domination. *Impregnational selection.* Dimensional selection. Structural selection. Potential selection. Fecundal selection.		*Institutional selection.* Ecclesiastical selection Military selection. Sanitary selection. Penal selection. *Prudential selection.*

(9) *Environal selection.*—As environal selection involves not only the superior propagation of the better fitted, but the inferior propagation of the less fitted and the non-propagation of the least fitted, it may be described as the *exclusive propagation of those better fitted to the environment through the failure to propagate of the less fitted.* Transformation by means of environal selection depends on the varying degrees of adaptation to the environment in creatures that are intergenerating, the higher degrees being possessed by other than average forms. Divergence is produced by environal selection only when to the above conditions producing transformation are added causes that prevent intercrossing between the sections that are being independently transformed. In other words, *independent environal selection produces divergence.*

(10) *Sexual selection* is the exclusive propagation of those better fitted to the sexual instincts of the species through the failure to propagate of the less fitted. In the words of Darwin, "It depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction."* It is the form of reflexive selections which has received Darwin's attention, and is consequently familiar to all. There are, however, certain points that need to be emphasized.

This is the principle in accordance with which correspondence is secured between the external characters and the sexual instincts of a species, and also between the instincts of the two sexes, in so far as they relate to reproduction. This result is secured partly by the failure to propagate of those whose powers of attraction and conquest do not reach the standard demanded by the instincts of the other sex and partly by the failure of those whose instincts diverge too widely from the typical characteristics of the other sex. For example, on the highlands of North China I have observed a species of creeping cricket of the genus Bradyphorus, the male of which calls the female by a sharp stridulation, to which the female responds by approaching the male and finally climbing upon its back. Now, we can well understand that the call of the male has been brought to its present shrill, penetrating perfection through the failure to attract mates in the case of males that were but feebly endowed, but it is equally certain that those females whose sluggish instincts have been capable of responding only to an unusually intense call have for the most part failed of leaving offspring, and, if any have been so unreasonable as to wait for the male to seek them out, they have, doubtless, perished without per-

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* "Descent of Man," p. 3 of Chap. VIII.

petuating their perverted instincts. If my view is correct, the change producing divergent sexual characteristics may be either in the instinct or in the characters with which the instinct is correlated. It seems probable that in the vast majority of cases the more strongly divergent forms have been reached by a multitude of deviations alternating between the psychical and the physiological and morphological characters of the species, the chief, indispensable condition being the prevention of interbreeding between the diverging sections of the species.

Sexual selection is sometimes referred to as if it were the influence of sexual instincts in giving character to the organs of a given sex, first by the instincts of the given sex rousing the individuals of that sex to successful activity in securing propagation, the degree of success depending on the degree of adaptation of the organs of the individual to the purpose of the activity (as in the case of barnyard cocks winning partners by the use of their spurs), and, second, by the instincts of the opposite sex being roused to successful action according as the endowments of the given sex are fitted to the end (as in the case of peacocks winning partners by the display of ornamentation). Starting, however, with this conception of the nature of sexual selection, we shall find great difficulty in obtaining from the principle any explanation of the origin of species or of divergent evolution of any kind. If divergent instincts are the causes of divergent forms, colors and qualities, what are the causes of the transformation of the instincts in lines that are persistently divergent? The problems of transformation and divergence are as far from solution after the application of the theory as before.

If, on the other hand, we recognize sexual selection as the harmonizing of the forms, colors, and qualities of a species with its sexual instincts and of the sexual instincts with its forms, colors, and qualities, we shall not claim that either set of characters is directly and continuously the cause of transformation in the other; but rather that the two sets play upon each other in such a way as to produce a state of *unstable equilibrium* in both sets, the result of which is indefinite transformation in the secondary sexual characters of each section of a species that constitutes a separate intergenerant, and that the independent transformation inevitably results in divergence. In Darwin's presentation of the principle of sexual selection, the chief endeavor is to show that differences in voice and ornamentation between males and females of the same species are probably, in a large degree, due to diversity in the action of sexual selection upon the different sexes; but this is a very different result from differences in the same respects between those of the same sex in closely allied varieties and species, and no clear understanding of the subject will ever be reached till those who study and discuss the subject discriminate between these two classes of phenomena. The formation of differences of the former kind is simple transformation without divergence, while the entrance of differences of the latter kind is divergent evolution tending to the production of separate species.

If a species deficient in secondary sexual distinctions, after being divided into segregated sections, attains a high development of such distinctions, it is easy to believe that they will be developed in different ways in the different sections, and that thus they will become specific distinctions; but it is not so easy to see why a species in which sexual distinctions have already been fully developed should undergo divergent changes in the different sections into which it may be divided. It is in such cases that we discover the important influence of what I have called *unstable equilibrium*. It seems probable that in some cases small differences originating through indefinite variation in only a few isolated individuals are seized upon by the exaggerating fancies of the other sex, and are thus first preserved through isolation and then exaggerated by sexual selection. In other words, *independent sexual selection produces segregation and divergence.*

(11) *Social selection* is the exclusive breeding of those better fitted to the social constitution and instincts of the race through the failure to breed of those less fitted. Social organization has reference chiefly to coöperation in securing sustentation and defense. If for each species there were but one possible form of social organization through which sustentation could be secured, there would be no need of considering social selection, for the form of social organization would be rigorously determined by natural selection, and the success of the individual through conformity to that organization would be sufficiently explained by the principle of natural selection. But different forms of social organization are often exhibited by the same or closely allied species; and we find that, in such cases as elsewhere, the prosperity of the individual is largely dependent on his conformity to the social organism to which he belongs. Social selection must, therefore, in some cases, have been an important factor in maintaining a correspondence between the capacities and the social organization of a race or species. When a species or a section of a species is undergoing a change of social habits, there will be individuals that fail through reverting to the old instincts and methods which put them out of accord with the rest of the community. But through the failure of these the inherited instincts of the race are brought into increasing

accord with the new habits till, in the case of most species, there are but few individuals that fail through lack of appropriate social instincts. Nevertheless, in the branches of the human species that have attained the highest civilization the process is still far from complete, for the instincts of many individuals are in conflict with civilized habits.

We find that the natural faculties that are best fitted to secure individual success, and a numerous and long-continued descent, are different under different forms of civilization. Social habits in a great measure determine the food and clothing of a community and thus deeply affect the qualities of the race. The degree of exposure to which the young are habitually subjected is also largely determined by social custom, and so the quality of the constitution that is permitted to survive. In other words, the form of parental selection that prevails in any community is often determined by social selection, as the form of social selection is sometimes determined by natural selection. Many matters which, amongst irrational animals, are determined by instincts guiding the individual directly to the needed resources, and showing what provision must be made, are, with man, determined by social instincts, leading the individual to follow the general experience or traditional habits of his clan.

As in countries where there are no beasts of prey the gregarious instinct of cattle ceases to be a necessity for the preservation of life, it is no longer maintained by natural selection, but it may be preserved by social selection; for though occasional stragglers appear, they are, through lack of adaptation to the social organization, specially liable to fail of finding mates, and, therefore, to fail of propagating their kind. Between the capacities of a community and its social organization there is a constant action and reaction which tends with more or less rapidity toward transformation; and this tendency is increased when a small community, during a long separation from other communities, gradually increases in strength, independently constructing a civilization of its own. In other words, *independent social selection tends toward divergent evolution of capacities and of social organization.*

(12) *Filio-parental selection* is the exclusive breeding of those better adapted to the relations in which parents and offspring stand to each other, through the failure to live and propagate of those less adapted. How the power of giving suck and the corresponding instinct for sucking were first developed it may be impossible to tell; but it is evident that having once been established as the method of sustentation for the young of mammals, any young lacking the instinct would perish without leaving descent. There is every reason to believe that,

with the exception of a few of mankind, and still fewer of domestic animals, it may be truly said of every individual mammal that all its ancestry, through all generations since they became fairly mammalian, have had this instinct in full force; and yet it sometimes fails and the line of descent is cut short with the individual that fails. Till comparatively recent times the same was true of man; but we now find some cases in which the young survive in spite of their inability to suck, and the constancy of this mammalian characteristic is being gradually impaired. There is also in some races an increasing tendency to shorter periods of lactation, or to the entire suppression of the function; so that it seems not improbable that there may yet arise a variety of the human species in which the power will be comparatively obsolete. Under such conditions the instinct for sucking would cease to be of any advantage, while special advantage would accrue to those best able to thrive on the artificial food habitually provided by the parents. In some countries this would be the milk of ruminating animals, while in other countries it would be some vegetable preparation. Through this diversity in the food provided by the parents for their infants and small children, there is even now a constant diversity in the parental selection prevailing in different countries. Diversity in the forms of parental selection is also produced by diversity in the clothing and artificial heat provided by parents; in the protection, on the one hand, of children from the wind and rain and direct rays of the sun, and on the other hand, their exposure to the same with shaven heads or naked bodies; and in the methods of binding, cramping, and mutilating the head, feet, waist, and other parts of the body. From this point of view we see how largely the form of parental selection is determined by social custom, and how it is sometimes enforced by social selection, which excludes from the benefits of the caste or tribe all who have not passed through the ordeal.

As filio-parental selection is due to different degrees of adaptation between the parent and offspring, it may be characterized not only by fatal departures in offspring from the characters required in their relations to their parents, but by fatal departures in parents from the characters required in parents in their relations to their offspring. As an example of the former, we may refer to the death at birth of children with excessively large heads; and as an example of the latter, to the death at birth of all the children of a mother with a contracted pelvis.

(13) *Dominational selection.*—Variations that are equally fitted to cope with the environment may be divided into two classes—those better able and those less able to cope with other members of the species in the appropriation of resources. Increase of population and

the consequent competition between members of the same species condemns the latter to premature death, or at least to failure in propagating, unless they find new resources by migrating or by changing their habits. Competition between kindred for the possession of identical resources we find directly connected with two quite distinct principles of evolution: (1) With the principle of *dominational selection* tending to discriminate between those equally adapted to the environment, through the success and consequent propagation of those only that are best able to cope with their kindred in appropriating advantages; (2) with the principle of *competitive disruption*, tending to break up old relations and old habits, and so preparing the way for the formation of new habits producing segregation and divergence. The latter of these principles was referred to at the end of Section III of my paper on "Divergent Evolution through Cumulative Segregation." The first I now briefly describe, without attempting to show its important influence on the transformation and divergence of species.

Dominational selection is the exclusive breeding of those better able to appropriate natural resources or mates, or the provision made by parents of society, not through being better fitted to the environment or to the organized methods of coöperation and assistance, but through being better able to overcome or outdo their rivals of the same species. It results from the contest or rivalry with each other of members of the same species that are equally fitted to the environment and to the constitution of the species and the consequent failure of all that are not able to cope with their kindred. "The law of battle" is a form of dominational selection which Darwin emphasizes as having great influence in determining what males shall have the best success in procuring mates. But there is a similar law determining what individuals shall obtain the resources furnished by nature or elaborated by parents and society. We may have dominational selection relating to sustentation, protection, and nidification, as well as to the possession of females. And in gaining a single end there may be a great variety of dominating methods. Combat between males for the possession of females is not found in the vegetable kingdom; but the prepotence of the pollen of certain flowers over that of other flowers of the same race may play a similar rôle. This we may call *prepotential domination.*

Dominational selection differs from natural selection in that it does not depend on degrees of adaptation to the environment, and from other forms of reflexive selection in that it depends on a special form of the relationship in which members of the same species stand to each other. It seems desirable that this form of selection, which depends on adaptation for overcoming, outdoing, or supplanting others of the same species, should be clearly distinguished and named. We further note that there can be no doubt that dominational selection acting for many generations on sections of a species that are prevented from intercrossing will in all probability follow somewhat different lines. In other words, *independent dominational selection will produce divergent evolution.*

(14) * *Impregnational selection.*—The coördination between the pollen of a given species and the stigma and ovules of the same species must be kept up by a process of selection, resulting from the failure to propagate of the individuals whose pollen is least potent, and of those whose ovules are most difficult to fertilize. This we may appropriately call potential selection; and it will be convenient to class it with forms of selection securing other coördinations necessary for successful impregnation. These other forms are: dimensional selection, of which we have an example in the coördination between the length of the pollen tubes and of the pistils; also fecundal selection, illustrated by the different degrees of survival secured by variation in the number of the ovules and in the quantity and methods of distribution of the pollen grains; and, as illustrated, in many species of insects, structural selection, due to the success gained through superior coördination of the organs by which males and females clasp each other. Impregnational selection is an important form of reflexive selection. I wish here to call especial attention to the importance of fecundal selection.

(15) *Fecundal selection* produces intensive segregation with divergence through independent *fecundal intension,* in isolated sections of a species. It is the form of selection that results from propagation according to degrees of fertility. As it involves not only the superior propagation of the more fertile, but the inferior propagation of the less fertile and the non-propagation of the least fertile, it may be described as the exclusive propagation of the more fertile through the failure to propagate of the less fertile. It would avail nothing in determining the form that is to prevail in succeeding generations if it did not in some degree preclude the crossing of the less fertile with the more fertile; but, as it is evident that, so long as increased fertility is not a disadvantage, the more fertile half of the species will leave a larger number of offspring than the less fertile half, it follows that when the offspring have come to maturity a larger portion of the fertile will consort with the fertile than in the previous generation; and so the fertility of the following generation will be still further increased. The chief check to this law of *cumulative fertility* is found in the correlative law of cumulative adaptation through adaptational selection. *The combined action of these two laws results in the triumphant development of the most fertile of the best fitted or the best fitted of the most fertile.*

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*As this paragraph does not occur in the original paper it is printed in different form.

Another result from the combined action of these two laws is that, *in species well adjusted to the environment, the typical, that is the average, form of the species is not only the best adapted, but it is the most fertile;* and this correlation between fertility and adaptation in the average form of the species or race is a strongly conservative principle, tending to prevent the rapid transformation of the race or species. Giants, dwarfs, and extreme departures from the type of other kinds are more likely to be sterile than the typical form of the species; and therefore if, through change in the environment or in the social conditions, some extreme form has an advantage in gaining subsistence, it will usually fail of propagating its kind with the relative rapidity of the less-favored average form. This is at present true of highly intellectual variations of civilized man. Those of moderate capacities are more prolific and accordingly persist, though less successful in other respects than the intellectual. But so long as the most successful individuals are those surpassing the average in intellectual endowment, so long will the average endowment be more or less steadily advancing; for, of intellectual families, those that are fairly fertile will leave more impress on succeeding generations than those that are sterile; and of fertile families, those that are above the average in intellect will have the advantage in leaving descendants to inherit their endowments.

(16) *Institutional selection* is a form of exclusive breeding closely related to social selection, but differing from it very much as artificial selection differs from natural selection. Institutional selection is the influence of institutions, customs, and laws in determining what classes of individuals have an opportunity to raise children. In most civilized countries criminals convicted of important offenses are usually so confined as to prevent their adding to the population of the community during the time of their confinement. This is a method of improving the race that might be carried farther than it has been. In some countries the insane, the imbecile, and lepers are confined in asylums and not allowed to marry, and in other countries ecclesiastical and military restrictions prevent certain portions of the community from raising families.

(17) * Prudential selection is due to the delay of marriage and other methods of limiting the number of children for prudential reasons.

(18) *Result of the foregoing survey of selectional intension.*—The analysis we have now completed shows us that certain changes in the form of selection are due to changes in the environment and that others are

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*As section (17) does not occur in the original paper, it is printed in different form.

due to changes in the organism. We find: First, that all the forms of reflexive selection are due to the relations of members of the same species to each other, and are liable to change without any change in the environments; second, that active selection is due to change in the successful use of the powers of the organism in dealing with the environment and is not dependent on change in the environment; third, that passive selection, which is due to the exposure of the organism to a different environment, is often produced by the organism's entering a new environment without there being any change in either the new or the old environment; fourth, that though passive selection is produced by change in the environment, the more effective forms of selection do not appear till the organism has so multiplied as to produce what I call "dominational selection" through intense competition between rival individuals of the same species in gaining possession of limited resources; and fifth, that passive selection, which depends on change in the environment, also depends on variations in the adaptations of the organism.

(19) *In this enumeration of the different forms of selection I have introduced certain divisions that are not given in the paper as read before the Linnean Society in 1889. These are structural, dimensional, and potential selection (which I have grouped with fecundal selection as forms of impregnational selection), and prudential selection, which stands by itself; fecundal selection was discussed in the paper as originally published, under the term "fecundal intension." As having an influence on survival, I now recognize it as belonging among the forms of selection. The active principle may appropriately be called fecundal selection, and the effect it produces on an organic group may be called fecundal intension.

In preparing my table of the forms of selection I have found difficulty in deciding where natural selection should be placed, and how wide a definition should be given to it. Some biologists use it as including sexual selection, while others agree with Darwin in considering sexual selection as belonging to a very different sphere, seeing that changes in sexual selection depend on changes in the activities of the organism and not on changes in the environment. But appeal to Darwin's writings does not remove all difficulty; for, if we decide that Darwin does not include sexual selection under natural selection, it still seems certain that he considered certain forms of what I have called dominational selection as forms of natural selection. But dominational selection is as decidedly reflexive in its action as is sexual selection. If, then, sexual selection is separated from natural selection, should not dominational selection also be considered as distinct?

As Darwin has in several places stated that natural selection is subject to change only when external conditions change,† I have classed it as that form of environal

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* As section (19) does not occur in the original paper, it is printed in different form.

† See Origin of Species, in the two chapters on geographical distribution, ed. 6, especially on page 355, where Darwin discusses the divergence of closely allied species on islands within sight of each other.

selection which is controlled by activities belonging to nature outside of the species. It is, therefore, clearly distinguished from active (or endonomic) selection, which is controlled by differences of aptitudes or of habitudes in the different groups for dealing with the environment, and not by exposure of the different groups to different environments.

9. *Indiscriminate Eliminational Intension.*

Eliminational intension is segregation and divergence produced by the indiscriminate destruction or failure to propagate of a part of the individuals of an intergenerating section of a species. Though indiscriminate destruction can not be classed as a form of natural selection, it may nevertheless be the cause of transformation; and when a species is distributed in sections that are prevented from intergenerating, divergent evolution will often be hastened by the indiscriminate destruction of part of the members of one or more sections. If a species inhabiting a large island is divided by geological subsidence into two large sections, there may be a very close resemblance in the average character of the two sections; but if a subsequent eruption of hot ashes destroys a large portion of the individuals of one section, or of both, the probability of a close correspondence in the average character of the two sections will be very much less than before the eruption.

Again, when the area occupied by a species is divided into two or more large districts, the occupants of which can have little or no opportunity for crossing, divergent evolution will arise in the different districts unless there is some constantly operating cause that insures that all the varieties surviving and propagating in any one district shall survive and propagate in all the districts. No such cause has ever been pointed out, but, on the contrary, it can easily be shown that the probability is very small that such a correspondence would occur, even if at the time of the division of the areas every individual in each district was represented by a completely similar individual in each of the other districts. Let us suppose a case:

(1) Suppose the creatures under consideration to be a species of mollusk, the sexual instincts of which act without any segregative tendency between the varieties of the same species, there being no aversion or other impediment that interferes with the free crossing of all the variations occurring within the limits of one district.

(2) Suppose that the number of individuals in each district is 10,000,000.

(3) Suppose that one in a thousand of these has a tongue strong enough to feed on the bark of the tree the leaves of which are the ordinary food of the species, and that one in a thousand is capable of

digesting the same, so that, in each district alike, one in a million could survive in this way though the crop of leaves should fail.

(4) Suppose that there are, through diversity of adaptations of this kind to products of the environment, ten different kinds of accessible forms of food, on each kind of which one in a million of the individuals of each district might feed if driven by necessity.

(5) Now suppose the same necessity should occur in each district through the destruction of the leaves on which they habitually feed, and that there are accordingly in each district a hundred survivors able to maintain themselves on other kinds of food.

Under such circumstances (the correspondences of which we have in our supposition made much more exact than the actual deviations from a mean ever present), even under such circumstances of completely parallel variation, what is the probability that in each of the separate districts the few that would meet with other individuals and have an opportunity to propagate the species would be similarly endowed and similarly related to the environment?

In order to still further simplify the problem, let us assume that in the case of each kind in each district the probability that it will succeed in propagating is exactly balanced by the probability that it will fail. The probability, then, that any given number, a, of the ten kinds in a given district will succeed is found by estimating the number of ways in which a things can be taken out of 10 things, and dividing this number by the tenth power of 2, that is, by 1024. This is completely parallel to the number of ways in which ten pennies can be arranged as to head and tail, each penny representing one form of variation, and its lying head-up indicating success in propagating. In 1024 experiments the probability is—

That 0 will succeed........	1 time	That 6 will succeed.........	210 times
That 1 will succeed........	10 times	That 7 will succeed	120 times
That 2 will succeed	45 times	That 8 will succeed.........	45 times
That 3 will succeed........	120 times	That 9 will succeed........	10 times
That 4 will succeed........	210 times	That 10 will succeed........	1 time
That 5 will succeed........	252 times		

These figures are found in the eleventh line of what is known as the "Table of the Binomial Coefficients," or the "Arithmetical Triangle."* And so in the case of any number of objects, the number of combinations that may be made with n objects is found in the $n + 1$th line of the arithmetical triangle classified according as there are 0, 1, 2, 3, or more objects in each combination. The whole number of combinations may also be found by calculating the nth power of 2.

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* See "Principles of Science," by W S. Jevons.

The possible combinations of the ten varieties in question, any one of which is as likely to occur as is any other, are 1,024, which is equal to 2 raised to the 10th power; the probability, therefore, that the combination or set of varieties that succeeds in one district is $\frac{1}{1024}$, or 1 in 1,024; while the probability that those that succeed in the one district will not be all the same as in the other will be $\frac{1023}{1024}$, or 1,023 in 1,024, which is more than a thousand times greater than the reverse probability.

These 1,024 different results, any one of which may occur in one section, are calculated on the supposition that all the representatives of the species in one section that succeed in propagating will in time coalesce by intercrossing; as we shall presently see, the number of divergences in the two sections may be vastly increased by the diversity of ways in which the same varieties may be combined through the greater or less influence of minor segregations within the bounds of each district.

10. *Amalgamational Intension.*

In my paper on "Divergent Evolution through Cumulative Segregation," I have referred to the fact that the vast majority of divergent forms produced by segregation, after existing for a time, are interfused with competing forms of the same species. Now, it is evident that when a permanent segregation arises, if in the separate sections there is a diversity of amalgamations between the slightly divergent forms produced by partial segregations, the results will be divergent in these separate sections. That there will be diversity in this respect, we may argue, first, from the improbability that all the varieties in any one section will occur in each of the other sections; second, from the improbability that if the same varieties occur in each section they will occur in the same proportions; and, third, from the improbability that if they are the same and in the same proportions, they will break over the barriers and breed with each other in precisely the same way in each section. Amalgamational intension relates only to the last point. The other two points have been discussed under the principle that separation always involves more or less segregation (see the third paragraph on the first page of this paper), and under indiscriminate elimination, which we have just been considering.

Taking up, again, the supposed case considered under eliminational intension, if the different kinds of new food were so situated as to make it more or less difficult for those feeding on one kind to cross with those feeding on other kinds, the representatives of the species in each of the completely separated districts would be divided into minor segregations of a partial kind; and the different degrees of intercrossing between the minor segregations in the separate districts would be an additional cause of divergence, which we may appropriately class as a form of amalgamational intension. Occasional interchange of stations by the varieties in one district would produce a degree of homogeneity in the forms of one district that would not be found when comparing those of different districts; but as the degrees of intercrossing between any two or more identical varieties that might happen to be preserved in both districts would, in all probability, differ in different districts, the correspondence that at first existed between certain portions of the two sections would gradually disappear.

11. *Combined Influence of these Principles.*

We have not at present sufficient knowledge of the influence of each of the principles of transformation to enable us to estimate their comparative importance; but we know enough of their combined action to anticipate with confidence that wherever separate or segregate generation arises, producing more or less divergence, there these principles will in time intensify the result. The transformations and divergences of nature are produced by the interplay of numerous factors most intimately combined, and though for the purpose of comprehending the process we are compelled to study each principle by itself, we must remember that in nature they not only combine, but combine in a vast variety of ways. There is, however, reason to believe that species sometimes become so devoid of plasticity that nearly all transformation is precluded, and, if the environment is greatly changed, even in the most gradual manner, extinction is the result.

II. DIVERGENCE IN MOLLUSKS.

1. *Divergent Evolution in the Land Mollusks of Oahu.*

Oahu is one of the Sandwich Islands, or Hawaiian Islands, as they are now usually called. It is of volcanic origin, but the two mountain ranges, which lie one on the northeast and the other on the southwest side of the island, show no signs of recent volcanic action. Unlike the mountains of Hawaii and East Maui, their sides are very deeply furrowed by the action of water, and their forests are not broken by flows of lava. The forests of the islands cover these two ranges, forming two disconnected strips, the one about 36 and the other about 18 miles in length. In these forests are found many hundred varieties, representing over 200 species, belonging to 8 genera, of the Achatinellidæ.

Two of these genera, Amastra and Leptachatina, are, for the most part, found under the dead leaves of trees in damp places; and one, Laminella, is found chiefly on low shrubs, while the remaining five genera are always found on trees or shrubs. Now, it must be remembered that the climate is tropical, and that the rainfall is so distributed through the year that in the shady groves there is nothing to drive the arboreal species from their haunts on the leaves or branches of the trees. Still further, as this family, unlike most other land mollusks, produces its young, not from eggs, but in a living, active form, there is no occasion in its life history that requires it to leave the tree in which it lives from generation to generation. In the distribution and divergence of these varieties and species we learn the following lessons:

(1) *Varieties are incipient species, and species are strongly pronounced varieties.* A full collection of the varieties and species of any polymorphic genus produces an oppressive sense of confusion on the mind of anyone who examines it for the first time. This is preëminently true of a full collection of the Achatinellidæ of the island of Oahu. Eight genera are represented by a multitude of varieties and species which, within the limits of each genus, are, for the most part, completely intergraded with each other. As natural selection has not removed the intermediate forms, it is impossible to say where a species begins and where it ends. Having selected a given form as the type of a given arboreal species, we soon find that it inhabits perhaps only one or two valleys, say half a mile in width, and only one, two, or three miles in length. Beyond these limits it is represented by varieties that become more divergent as the distance from the home of the type increases; and, in the case of the Achatinella and Bulimella, this difference is so great that in districts eight or ten miles apart every one will admit that the forms all belong to different species. Indeed, in many cases, though the same vegetation is present, the habits of feeding have changed, while in other cases the form and color have changed while the habits remain essentially the same.

Though it is easy to find degrees of divergence which most naturalists will agree in calling specific, but which in a full collection are shown to be completely intergraded, yet if a full collection of the different forms should be submitted in succession to a hundred different naturalists to classify, it would be found that no two would agree as to the number of species, and a still greater diversity of opinion would be revealed as to where the limits of the different species should be placed. This is exactly what we might expect if varieties are incipient species, and species are simply strongly developed varieties. Such being the case, it is folly to ask that the nomenclature should be based on some fundamental distinction between species and varieties.*

The best nomenclature is the one in which the specific distinctions correspond in degree with those that are recognized as specific in other families, and in which a degree of divergence that is considered specific in one part of a genus is considered specific in every part. If the distinctions on which Reeve, Pfeiffer, and Newcomb have founded the species in Makiki and Manoa are received as specific distinctions, then similar distinctions occurring in the forms of other valleys must be recognized as belonging to different species. I by no means contend that these differences should be regarded as specific; but having received the three or four forms of Achatinella found in Manoa as good species, it will not do to say that the forms of Achatinella found in Waialei, differing from each other in the same manner and degree, are but one species.

Notwithstanding the diversity of opinion that will always exist as to how many species should be made of the forms occurring in any one valley, every one will agree that the forms of Bulimella and Achatinella found in any one valley are quite distinct species from those found in valleys that are ten or twenty miles distant. The lessons we are drawing from the divergence in this family are, therefore, not dependent on any special views concerning the number of species that ought to be received.

As examples of intergrading species, examine first the types of *Achatinella producta, A. adusta*, and *A. buddii* from Makiki; then all the forms of these and the other species of Achatinella found in Makiki, and then the forms found in the successive valleys of the whole mountain range.

If freedom from intergrading is received as the necessary and sufficient test of good species, then a multitude of forms that are only varieties may be turned into good species by burning the forests in alternate valleys on either side of this mountain range. Moreover, if this is the true test of species, the species-maker who throws intergrade forms into the fire is quite consistent, even if not quite frank.

Whether we call these divergent forms species or varieties, the process by which the divergence has been produced is a matter of equal interest. Indeed, some evolutionists maintain that one of the chief desiderata in the theory of evolution is an explanation of the origin of varieties.† Variations are deviations from the average, but varieties

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*So far as the necessary material can be obtained the statistical method of testing species is under such conditions the best.

† See "Evolution and its Relations to Religious Thought," by Joseph Le Conte, published by Appleton & Co., p. 252

are groups of individuals in which the averages differ, and in which the inheritable characters differ. Still further, it is usually admitted that the divergences presented by varieties are not always essential to the well-being of the forms that possess them, and that in many cases the forms that are confined to separate localities might exchange positions without suffering disadvantage. Divergence in these initial stages has seemed to many to be an obscurer problem than the advancing usefulness which sometimes entirely remodels an organ. For as Professor Le Conte has said, "Natural selection does not make an organ useful, but only more useful."

I believe the theory of divergent evolution, presented in this and the preceding paper, is applicable to the formation of divergences during the stage when some of the differences, if not all, bring neither advantage nor disadvantage to those that possess them. Whatever we call these divergent forms, can we give any explanation of the causes that have produced them?

(2) *Divergent evolution does not necessarily depend on diverse environments.* In other words, it does not necessarily depend on change in the conditions surrounding the organism, or on the organism being brought into a district presenting a different set of conditions.

Darwin maintains that isolation (by which he designates geographical separation), without any differences in the surrounding organisms or in the physical conditions, presents no occasion for divergence of character. He says, "If a number of species, after having long competed with each other in their old home, were to migrate in a body into a new and afterwards isolated country, they would be little liable to modification." (Origin of Species, 6th ed., p. 319.)

Spencer expresses the same idea by saying that "Vital actions remain constant so long as the external actions to which they correspond remain constant."* There must be maintained a tolerably uniform species so long as there continues a tolerably uniform set of conditions in which it may exist." (See Spencer's Principles of Biology, sections 91, 156, 169, 170.) In other words, divergence of character in the descendants of one stock occupying different districts does not arise except as it is preceded by difference in the physical conditions, or in the surrounding organisms, of the different districts. After molding this thought in many forms, Spencer makes it the fundamental principle on which he builds not a small portion of his philos-

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* Though apparently opposed to his theory of "the production of certain local forms by amixia," this same idea is found in Weismann's "Studies in the Theory of Descent," pp. 109–115 (English edition).

ophy. Darwin is more guarded in his statements; still, as we have already shown, he sometimes seems to reason from an assumption quite in accord with what Spencer would have us receive as essential to the very idea of causation in vital processes. For example, his explanation of the fact that on the different islands of the Galapagos Archipelago one genus is, in many cases, represented by several closely allied species which are undoubtedly modified forms of one continental species, seems to rest on the assumption that if every species that gained access to any island had at the same time gained access to the other islands of the archipelago, there would then have been no occasion or opportunity for the divergences we now find. (See Origin of Species, 6th ed., p. 355.)

It seems to me that the divergences presented by the varieties and species of the family Achatinellidæ are at variance with this assumption. Not only are islands in sight of each other occupied by divergent species, but different parts of the same mountain range exposed to the same winds and rains and clothed with the same vegetation are the homes of divergent forms.

Turning to the map of the island of Oahu, we find a mountain range extending 36 miles from northwest to southeast, nearly parallel with the northeast coast. The northeast side of this range is exposed to the trade-winds fresh from the ocean, and accordingly receives a heavier rainfall than the other side; but there is not much difference in the amount of rain received by the different valleys on one side of the mountain. In nearly all these valleys on either side of the range are found shady groves of what the natives call the "kukui" (*Aleurites triloba*). Many species of the genera Achatinella and Bulimella have their haunts in these groves, some species clinging to the leaves and young branches, and others to the trunks and the larger branches. Most of the species thrive only where the shade is dense and the atmosphere laden with dampness a large portion of each month.

The student who starts with the assumption that divergent varieties and species arise only through exposure to different environments will expect that these groves, at least those on the same side of the mountain range, will be occupied by the same species. Having found one set of species in a given valley, when he comes to a valley ten miles distant, possessing the same conditions of soil, rainfall, vegetation, and shade, where the birds, reptiles, and insects are the same, where the mice and ants, their only known enemies,* are the same, he naturally looks on the leaves and branches of the familiar trees for

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* The species that molest the snails were not known on these islands till comparatively recent times.

the snails he has found in similar stations not far distant; but what is his surprise to find only different species, all allied to, but quite distinct from, those he has previously known! Twenty miles from the first valley he renews his investigations, finding the forms of all the different groups still more divergent, though all the conditions of the environment are, so far as he can observe, the same.

He finally perceives that he must give up the theory that the cause of this divergence is exposure to different environments.

(3) *When the environment is the same in two districts occupied by allied species or varieties, it is evident that the differences that distinguish the latter can not be advantageous, even though their differences include strongly contrasted habits.* For in order that these differences should be advantageous, it is necessary not only that they should relate to the performance of vital functions, and, therefore, be differences of adaptation, but it is necessary that these differences of adaptation should relate to differences in the environment, so that the forms would be at some disadvantage if they should exchange districts. Advantageous differences are always adaptational; but adaptational differences are not always advantageous, and in such cases the divergence can not be primarily attributed to diversity in the action of natural selection in the different districts. Under the protection of isolation, diversity of selection may arise which helps in producing divergence; but when the environments are the same, the divergence is in no sense advantageous; for, if a given combination of characters is an advantage in one district, so would it also be in the other district, and the difference or divergence is no advantage.

A familiar example will perhaps put the distinction between the causes of survival and transformation and the causes of *divergent* survival and transformation in a clearer light. The forms of language are growths that are governed by the laws of utility as fully as the forms of varieties and species. Each language and each part of a language exists and persists only as it is found to be of use. The "survival of the fittest" is a law that is perhaps as conspicuous in the domain of language as in the organic world. Again, every language, like every organic species, is in many respects determined by the environment. A language, for example, developed in Java will present names for many plants and animals that will not be represented in a language developed in Greenland. But, granting all this, does it follow that linguistic differences are necessarily advantageous? The Polynesian system of counting by fours, and the Eskimo system that proceeds by scores, are undoubtedly useful systems; but is there anything advantageous in the difference? I think not, for each system is as well adapted to the environment of the other as to its own environment. We may look upon the more important parts of a language as persisting through their usefulness, the survival of the fittest being the law; but the divergent evolution which brings several languages out of one seems to be principally due to other principles which are closely akin to the principles that produce divergence in the organic world. *The fundamental condition in both organic and linguistic divergence is isolation; and, this being secured, diversity of habits, bringing diversity of aptitudes and diversity in the forms of survival, is sure to arise even when the environment is the same.*

(4) *Specific differences are not always differences of adaptation to the environment, and those that are not should not be attributed to the action of natural selection.* It is admitted by every one that a distinction relating to a character that is of no use in the economy of the organism can not have arisen under the influence of natural selection. Those who maintain that all specific distinctions are due to natural selection maintain at the same time that these distinctions are adaptational and advantageous. There are naturalists who maintain that the very essence of the Darwinian theory is "that specific differences must be advantageous,"* and, therefore, adaptational, while they do not claim the same for generic, family, and ordinate distinctions, or, indeed, for varietal distinctions, if I rightly understand. I have never seen any attempt to explain this supposed exception in the midst of the taxonomic series; and it seems to me that the break in the continuity of nature which this interpretation of the Darwinian theory supposes should lead us to a very careful investigation of the facts before we accept it as a true interpretation of nature.

I shall content myself with pointing out one distinction, occasionally occurring between allied species, for which no use has ever been, or is likely to be, found. I refer to the distinction between what are known as dextral and sinistral forms. This distinction relates to the form of the twisting of the animal and its shell. It is most easily recognized by holding the shell with the aperture toward you with the apex turned upward, and observing whether the aperture lies on the right side of the central columella of the shell or on the left. In the first case it is described as dextral, in the second as sinistral. In most families and genera of water mollusks the sinistral form occurs only as a sport (as in man the heart is sometimes found on the right side), and even among air-breathing mollusks the dextral form vastly predominates. Of the Achatinellidæ, Amastra and Leptachatina,

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* See letter from Mr. W. T. Thiselton Dyer, in Nature, vol. XXXIX, p. 8

which are genera of terrestrial habits, are (with but few exceptions) dextral in form; while the other genera, which are plant feeders and constantly hanging to branches or leaves, present many species that are constantly sinistral, and many others that are both dextral and sinistral. Why should *Achatinella adusta* in Pauoa and Makiki be constantly sinistral when the most nearly allied *A. producta* found in the same valleys is both dextral and sinistral? Why should *A. bacca* and *A. abbreviata* in Palolo and Waialae be constantly dextral when other species of Achatinella in the same valleys are for the most part sinistral? Is there any adaptation to the environment possessed by a dextral form which would be lost if the form was reversed? If not, natural selection could not have anything to do with that part of its character. *Bulimella rosea* is sinistral, while *B. bulimoides* is dextral. If in this respect they should exchange forms, would any disadvantage be experienced by either species? It is impossible to conceive of any disadvantage that would follow, and, therefore, I can not believe that this difference in the two species was in the first place due to natural, sexual, or any other form of selection.

There are many other specific distinctions presented in this family which seem to be of no advantage, though they are not so far removed from all suggestion of the possibility of use as the character we have just been considering. The brilliant colors and varied patterns presented by many of the arboreal species would be of advantage to themselves if they served as warning of nauseous qualities to creatures that are liable to prey upon them; but no such conditions exist. The birds of the forest region are for the most part fruit and nectar feeding; and the ants and mice which in recent years have made sad havoc with the mountain snails unfortunately do not spare the highly colored species.

There can be no doubt that when representatives of different genera occupy the same trees they remain segregated through the influence of sexual instincts, which must be associated with some means of recognizing those of their own group; but it is not at all probable that the colors and patterns of any species are recognized by their mates, or have been developed under the influence of sexual selection. There is, therefore, strong reason to doubt whether selection of any kind has been concerned in the production of the beautiful colors and patterns of these species, unless possibly correspondences in color within the limits of a genus are, in some cases, due to the inheritance of tendencies produced by selection when conditions were very different from what we now find. But the divergences in color and pattern in the species of one genus can not be thus explained.

(5) *The average radius of distribution for species of the same value in allied genera varies in the different genera directly as the average power and opportunity for migrating, and inversely as the plasticity and variability of each genus.* Comparing the distribution of the Helices of Europe with that of the Achatinellidæ of Oahu, the most striking contrast is found in the size of the areas occupied by the different species. *Helix pomatia* is distributed from England to Turkey, over an area 2,000 miles in length, while of the eight genera of Achatinellidæ on Oahu I know of but one species that seems to be distributed over the whole 36 miles of the main mountain range, and this one is represented by three varieties belonging to different parts of the range and perhaps worthy to be regarded as different species. The species to which I refer is *Auriculella auricula* (Fer.), the typical forms of which are found on the eastern half of the mountain range. On the other half of the range we find the closely allied forms to which I have given the manuscript names *solida* and *pellucida.* This great contrast in the size of the areas occupied must be due either to the greater plasticity of the Achatinellidæ or to their having inferior opportunities for migrating, or to both causes. As I become better acquainted with the great difference in the habits and circumstances of the contrasted species, I give increasing weight to the difference in the opportunities for migrating. With the continental species, floods must be one great means of distribution; but in the case of the insular species, the floods would carry floating individuals upon the grassland or into the sea, in either case to perish. Again, the habit of traveling upon the ground, which belongs to most of the Helices of Europe and America, gives incalculable opportunities for migration which are not enjoyed by species that are strictly arboreal, as are many of the Hawaiian species. Most of the Hawaiian snails are still further restricted in their opportunities by their inability to resist a dry atmosphere or exposure to the sun, which renders it necessary that they should remain in the isolated areas that are favored with shade in the different valleys.

The habits of the different genera occupying Oahu are also instructive as throwing light upon the relative areas occupied by the species of the different genera. Achatinella and Bulimella seem to be the most restricted in their opportunities for migrating; first, because they are entirely arboreal in their habits, clinging to the trunks and branches of trees through their whole life history; and, second, because, for the most part, they occupy the shady and damp thickets and groves, the shade in each valley being separated from similar shades in adjoining valleys by lofty and sparsely wooded mountain ridges at each side of the valley and by open grassland at the mouth of the valley. On the other hand, Apex, which for the most part occupies trees and shrubs on the ridges which are connected with each other through the central ridge of the mountain range, and Amastra and Leptachatina, which are for the most part found on the ground under dead and decaying leaves, seem to possess better opportunities for migration than either the Achatinella or Bulimella. Corresponding with these facts we find the species of Achatinella and Bulimella especially limited in the areas they occupy, while the species of Apex, Amastra, and Leptachatina are less so. For example, the area occupied by *Amastra turritella, A. tristis*, and *A. ventulus* includes the areas occupied by many species of Achatinella and Bulimella; and *Apex loratus* and *A. pallidus*, occupying the mountain ridges, range from Makiki to Halawa, exceeding the range attained by any arboreal species occupying the valleys of the same region.

(6) *When a group of divergent forms that are fertile with each other is being developed through the influence of local or geographical isolation, other conditions remaining constant, the number of forms that will be produced within a given area will vary inversely as the square of the average radius of distribution for the different forms.* As this average radius of distribution may be taken as the measure of the power and opportunities for migration, we may say that, other powers and opportunities remaining constant, *the number of species developed within a given area will vary inversely as the square of the average power and opportunities for migration.*

Though migration is in one sense a cause of isolation, it is evident that the number of isolated groups of individuals of a given form within a given area does not increase with the increase of migration. *Isolation is produced by the great contrast between ordinary and extraordinary combinations of opportunities for migration;* and this contrast is liable to be as great in the case of species that have limited powers and opportunities as in the case of those that have very great powers and opportunities. The number of isolations thus produced that can exist within the limits of a given area must vary inversely as the square of the power and opportunity for migration.

The facts of distribution we have been considering seem to correspond to this law.

(7) *Forms that are most nearly related, and are, therefore, the least subject to sexual and impregnational isolation, are distributed in such a manner that their divergence is directly porportional to their distance from each other, which is also the measure of the time and degree of their geographical isolation; while those most manifestly held apart by sexual instincts and impregnational incompatibilities do not follow this law.*

Bulimella is represented by two groups of species, one of ovate form, the other elongated and with the outlines of the spire less rounded. The widest divergence between these groups is presented by species occupying the same districts and valleys, but the widest divergences in the species of either of these groups are found in valleys widely separated. In the latter case, the degree of geographical separation is probably an approximate measure of the time and degree of isolation, and, therefore, the measure of the degree of divergence; while, in the former case, the isolation is probably as complete between forms occupying the same valley as between those of widely separated valleys. There is reason to believe that in the eastern part of the island these two groups are not fully held apart by sexual isolation or segregate fecundity and vigor, for there is complete intergrading, and the divergence between the groups in any one valley is much less than is found in the northwest portion of the island, where sexual incompatibility seems to be complete.

Achatinella bacca and *A. abbreviata* completely intergrade with each other, but they are associated with a number of other species of Achatinella with which they do not intergrade, prevented, it seems to me, by mutual incompatibility. We have, therefore, in the eastern valleys two groups of Achatinella completely segregated from each other, though occupying the same districts and in some measure the same stations; while in the other valleys the two groups coalesce, the different species occupying any one valley being only partially isolated by divergent habits of feeding.

The different genera and subgenera, which are undoubtedly segregated by divergent sexual instincts, as well as by physiological incompatibilities, are equally divergent, whether we compare forms from the same or from distant valleys.

(8) *The distribution of the varieties, species, and genera of Achatinella on this island is just such as would be produced by divergent evolution which depends on isolation as a necessary condition, even when the environments are different, and which always follows long-continued isolation, even when the environment surrounding the different sections is the same.*

It may be safely said of the multitude of varieties which inhabit the island of Oahu that every one is more or less segregated from all other varieties; and I believe this will be found true concerning varieties in every part of the world. This fundamental fact would probably never have been denied, except for the delusive idea that the advantage of divergence would lead to the accumulation of divergence even if segregation were entirely wanting. What could be a greater mistake for the breeder of animals than to imagine that by selecting extreme variations and breeding them together he would in time secure well-marked races? It must be equally at variance with fact to suppose that any advantage secured by divergent variations can be preserved and accumulated while the different forms are freely intergenerating.

In the family we are considering, the chief forms of isolation are probably what I have called local, geographical, industrial, and sexual isolation, strengthened in many cases by segregate fecundity and vigor. As illustrating local isolation I would mention varieties and species of Apex, for the most part occupying mountain ridges which are all connected with each other, without the intervention of geographical barriers. Geographical isolation is illustrated in the forms of Achatinella and Bulimella, which for the most part occupy the deep valleys, the ridges forming barriers that are very rarely surmounted. Industrial isolation is illustrated by the closely allied varieties of one group of species that occupy one valley, but are prevented from crossing by different habits of feeding. It is probable that sexual or seasonal isolation prevents the pairing of Achatinella with Bulimella when both occupy the same trees. Moreover, cross sterility would undoubtedly prevent the multiplication of the hybrids, if cross-unions ever do occur between forms so widely divergent. There can be no doubt that the same principles prevent the strongly marked groups of either genus from intergenerating; as, for example, in the case of *Achatinella bacca* and *A. abbreviata*, which are intergraded with each other, but not with the surrounding species of Achatinella.

Again, divergent forms of environal selection do not necessarily depend on exposure to different environments. Industrial isolation is produced by different modes of using the environment found in a single district; and the same cause will often produce diversity in the forms of environal selection affecting the isolated sections, distributed in different districts, but exposed to the same environment. Cumulative divergence in the methods of using the environment in the different sections of the species depends upon their isolation, and, therefore, increasing divergence in the forms of selection affecting the different branches depends upon their isolation. Geographical isolation under the same environment, if it does not of itself produce divergent forms of selection, opens the way for change in the habits of feeding, with diversity of selection in the different sections of the species. Take, for example, the species of Achatinella: In Manoa and Makiki they chiefly occupy the kukui (*Aleurites triloba*) and other trees, while in Kawailoa and that region they neglect the larger trees and take to the lobelia and other shrubs and herbaceous plants.

But why should the degree of divergence increase with the continuance of the isolation? The answer seems to be that the combined effects of the different principles of transformation in the isolated groups increase with the time of isolation; and, as independent transformation is never parallel, the divergence increases in the same ratio. Diversity of environal selection is undoubtedly one of the principles producing this divergence, even when the vegetation and physical conditions of the different districts are the same, for when the habits of feeding change, the environal selection must usually change. But there are cases of divergence accompanying isolation in which the habits of feeding seem to have remained unchanged; and in such cases I explain the divergence by the fact that any small fragment of a species is incapable of propagating all the qualities of the species in the exact proportion presented by the average of the species.

2. *Similar Facts in Other Regions.*

Many of the facts embodied in these eight propositions must have been observed wherever naturalists have studied the geographical distribution of the varieties and species of polymorphic genera; but in the distribution of the Achatinellidæ there are features of peculiar interest arising from the fact that the powers of migration possessed by the species of the surrounding environment are very much greater than those possessed by these molluscan species. Through this circumstance a comparatively uniform environment is produced in which the effects of independent generation unmodified by the effects of changed environment may be observed. The remarkable facts of distribution which we have on the island of Oahu are found in other parts of the Hawaiian Islands, wherever this family occurs. I am also fully convinced that, in other parts of the world, wherever one genus or family of very low powers of migration is surrounded by a body of plant and animal forms possessing much higher powers of migration, there similar facts will present themselves whenever investigation is made.

The distribution of land mollusks belonging to the genus Partula found on the Society Islands present similar features. The island of Reiatea, which is but 14 miles in length and 3 or 4 miles in breadth, is the home of about 30 species and varieties, most of which are confined to areas only a few square miles in extent. I am not informed as to the distribution of the plants on which these species feed, but there is no reason to suppose they occupy limited districts corresponding to those occupied by the different species of Partula.*

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* See Bulletin of the Museum of Comparative Zoölogy at Harvard University, vol. LX, No. 5.

III. DIVERGENCE IN INSECTS.

The dependence of divergence on some form of isolation is most clearly exemplified in insects, and though my studies are but limited in that field, I shall refer to a few cases, which may serve to direct attention to a class of facts of the highest interest not only to entomology, but to general biology.

1. *Divergence in Erynnis and Thanaos.*

Erynnis (*Pamphila*) *and Thanaos* (*Nisoniades*).—These two genera of small North American butterflies are worthy of the special attention of those who are studying the problems of divergent evolution, for they furnish strong indications that organisms which are with difficulty distinguished from each other by external form or color may, nevertheless, be well-established species segregated presumably by sexual instincts corresponding to sexual characters by which those of opposite sexes of the same species readily recognize each other, and probably cut off from the possibility of producing hybrids through incompatibility of physiological endowments. In the origin of some of these species geographical isolation may have had an important influence; but concerning others there can hardly be a doubt that the segregative influences, holding apart species that occupy the same districts, were, from an early stage, peculiarities of their sexual instincts and constitution. The reason for accepting this view of their origin is found in the fact that, though slightly divergent in other points, the characters by which they are clearly distinguished are found in the forms of the male genitalia; and in the characters of these organs we find clearly marked species, for the most part free from the intergrading forms which would certainly be presented if the different species were not prevented from crossing by sexual instincts or constitution.

A full description of these genera, with observations on the asymmetrical devolopment of the right and left sides of the genital armature in Thanaos, will be found in Scudder's Butterflies of New England. (See also Mem. Boston Soc. Nat. Hist., II (1874), and Proceedings of the same Society for April 27, 1870, vol. XIII (1871), p. 282.

2. *Divergence in Basilarchia.*

(1) Basilarchia (Scudder) is an attractive genus of butterflies peculiar to North America, where it is represented by four or five species. Three of these are found in New England, and are minutely described in Scudder's "Butterflies of New England," from which I draw my information (pp. 250-305).

The distribution of these three species is of great interest, as it illustrates divergence both with and without local segregation. *Basilarchia archippus* ranges over nearly the whole United States and over the southern portion of Canada. *B. astyanax* occupies the valley of the Mississippi and eastward to the Atlantic from the Gulf of Mexico on the south to the lakes on the north. *B. arthemis* is distributed from Newfoundland and Nova Scotia on the east, over New England, Canada, the region of the lakes, away to the northwest, toward the confines of Alaska. It will be observed that the area of distribution of *B. archippus* includes the whole of that of *B. astyanax* and a large portion of that of *B. arthemis;* while the areas of *B. astyanax* and *B. arthemis* overlap along the whole northern border of the territory occupied by *B. astyanax.* This area of overlapping distribution in which the three species are associated is about 1,000 miles in length and from 100 to 250 miles in width.

(2) *Forms of Isolation that separate Basilarchia archippus from B. astyanax and B. arthemis.*—It is evident that, in the present condition of distribution, geographical barriers and territorial separation have nothing to do with the integrity of *B. archippus* as a separate species. In other words, it is not under the influence of geographical or local isolation. Whatever may have been its past history, these certainly are not the causes that at present prevent it from interfusing with other species of Basilarchia with which it is associated.

Again, seasonal isolation seems to have but little influence; for though *B. archippus* seems to appear 15 or 20 days earlier than the other species, the remainder of the breeding season, which extends over many weeks, is coincident.

The habits and feeding instincts of this species must tend to separate it somewhat from *B. arthemis*, for this latter species frequents forest regions, especially when elevated and hilly, while *B. archippus* is found in the open country in fields and meadows, especially in low levels. The eggs of *B. arthemis* are chiefly deposited on the species of birch and willow that are found on the highlands; while the eggs of *B. archippus* are chiefly deposited on the willows and poplars found on the lowlands, though on the White Mountains it occasionally extends its range to as high levels as *B. arthemis.* There is, therefore, between these species a slight degree of industrial isolation; but this partial segregation does not prevent their being often found in the same fields, and unless held apart by sexual instincts and by partial infertility, hybrids, which are now very rare, would be very common.

We are, therefore, led to believe that diversity of sexual instincts, accompanied by a considerable degree of cross-sterility, is the chief cause preserving the independent character of this species. Except for the sexual segregation and segregate fecundity there is every reason to believe that this species could never have arisen, or, if it had arisen as a variety in some isolated locality, would have been submerged in the allied forms when its wider distribution was reached. This conclusion, which has been reached by observing the general relations of the species, is confirmed by a minute examination of the structure of the three species. We find that while the male genitalia of *B. astyanax* and *B. arthemis* differ but slightly, those of *B. archippus* are considerably divergent. This is an index of the psychological and physiological relations of varieties and species of no small importance; for a comparison of many species shows that differences of this kind are usually accompanied by corresponding degrees of segregation in sexual instincts and of cross-sterility. In other words, we find that difference in the male genitalia, which is a form of structural segregation, is an index of sexual segregation and segregate fecundity.

(3) *The Partial Isolation of B. astyanax and B. arthemis.*—In the relation of these two species we find examples of segregative influences differing somewhat from those that have just been found in the case of *B. archippus*. Regional isolation, with exposure to different climates and adaptations to different food-plants, has undoubtedly had an important influence in the formation of these species; but, in the part of the country where they coexist, their life-histories correspond completely, and cross-unions seem to be frequent. The hybrid form has been described as a separate species, and some entomologists have classed it as a dimorphic form of *B. arthemis;* but Scudder gives several reasons for believing that it is the result of cross-unions between these two species. There are, however, several reasons for believing that partial segregate fecundity exists between the two species; for, in the strip of territory where the two are associated they do not completely coalesce, as would be the case if they were completely cross-fertile. In Scudder's Butterflies of New England, pages 159 and 160, we find mention of two species (*Cercyonis alope* and *C. nephele*), in which the cross-sterility must be considerably weaker than between the two species we are now considering; for, in the intermediate region in which their areas overlap, the intergrade forms are comparatively abundant. Moreover, the difference in the male genitalia of *B. astyanax* and *B. arthemis*, though much less than that which appears when either of these is compared with *B. archippus*, is such as indicates a considerable degree of infertility.

In these two species we have, then, a good example of partial isolation through distribution over areas which, though overlapping, are for the most part distinct, reinforced by partial segregate fecundity which may or may not be accompanied by slightly divergent sexual instincts. There is also some isolation resulting from the fact that the plants on which *B. arthemis* seeks to deposit its eggs are chiefly the birches and willows of the hilly country, while *B. astyanax* prefers fruit trees of the Rosaceæ family and other plants that are found in the more open country. These are, as I have shown in my paper on "Divergent Evolution through Cumulative Segregation," exactly the conditions that produce, in successive generations, increasing degrees of segregate fecundity.

(4) *Cumulative Segregation in the Formation of the above Species.*—I judge that in the relations to each other of these three species we have the results of divergent evolution through cumulative segregation very clearly illustrated. In the earlier stages of divergence in this genus, *Basilarchia archippus*, with its fondness for the open fields, must have become partially separated from the parent form from which both *B. astyanax* and *B. arthemis* have since sprung. The separation may have been in some measure due to the methods of escaping from enemies; for we find that the form that has kept to the open country has through protective selection gained a very close resemblance to the coloring of *Anosia plexippus*, which is protected by its disagreeable qualities. The other form has probably gained compensative advantages by keeping closer to the woodlands. But the partial segregation thus produced would never have resulted in constant specific differences if segregate fecundity had not arisen between the two forms. We may believe that some form of impregnational segregation (either segregate structure, segregate fecundity, or segregate vigor) was early introduced, and that under the protection of this barrier the specific distinctions of the two forms became fully established, though even now the barrier is not so complete as to entirely preclude hybrids between *B. archippus* and each of the other species. Examples of both these hybrids are described by Scudder.

While this segregation was being completed, one of the two forms thus created must have become subject to a new set of segregative influences arising from wider distribution with diversity of climate and of habits of feeding, reinforced by a slight degree of segregate fecundity. *B. astyanax* and *B. arthemis* are the two species resulting from this last segregation, and the process is so far from being complete that wherever the areas of these two species overlap a hybrid form, which has been known as *B. proserpina*, appears. That it is a hybrid is proved by the fact that it "varies most toward *astyanax* where this prevails, and most towards *arthemis* where that prevails;" that it is found only in the narrow belt where the two species are brought into contact, and that it has been reported from so many points in this narrow belt that there is reason to believe that it occurs wherever the two species are brought into contact. If our exposition of the segregations to which these species have been subjected is correct, they are cumulative in two respects: first, because after one segregation has been established another is superimposed, and second, because a partial segregation established in one generation tends to become more complete in subsequent generations.

The primary causes in the whole process are the activities of the organisms acting upon each other and upon the environments in such a way as to produce, in the first place, independent generation with some degree of divergence, and then unbalanced selection of different forms producing transformation, which, acting upon sections of the species that are prevented from crossing, result in ever-increasing divergence.

3. *Divergent Evolution in the Periodical Cicada* (*Cicada septendecim*).*

In *Cicada septendecim* we have examples of two quite distinct divergences, each depending on its own forms of segregation, which are easily recognized.

The life history of this insect covers seventeen years and one or two months. The imago appears late in May, and for a little more than a month the males make the woods ring with their shrill stridulations. The eggs, which are deposited in the green twigs of trees, mature during the latter part of July, and each newly hatched larva, dropping to the ground, takes up a solitary subterranean life, which it follows till its period of seventeen years is nearly complete. It then appears above the ground, passes into its winged stage, and enters on a few weeks of social life which closes its career. This species is widely distributed in that part of the United States that lies between the Atlantic shores and the Rocky Mountains, but does not occur in Minnesota, Northern Michigan, or Northern New England. It is, however, represented by two races in every respect the same, except that one has a life-history of thirteen and the other of seventeen years. The thirteen-year race prevails in the Gulf States, but in New England and the Middle States the seventeen-year race is alone found. In Illinois, Missouri, Kansas, and in several of the Southern States the two races occur in the same localities; but it is evident that even in such localities it is only once in 221 years that there will be any opportunity for crossing between them, and we are informed by those who have made

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* My information is chiefly derived from Bulletin No. 8, Division of Entomology, U. S. Department of Agriculture, by Dr. C. V. Riley.

a special study of the subject that they do not cross when these opportunities occur; for 14, 15, and 16 year races are not found. These two races are, therefore, prevented from crossing by partial local isolation; by cyclical isolation rendering it impossible that a brood of each occupying the same locality should have opportunity for crossing more than once in seventeen generations of the shorter-lived race, or once in thirteen generations of the longer-lived race; and by sexual isolation that shows itself in diversity of instincts preventing them from pairing when other conditions favor.

Whether devices have been tried to induce cross-unions, and whether such unions are unfruitful, I have never heard; but the simple fact that fifteen-year forms do not appear in localities where the two races are found indicates that in nature they do not cross. Several such localities have been reported, but in none of them has an intermediate form been found. It seems, therefore, that we may safely draw the conclusion that we have here a case of complete sexual segregation between forms which to the human eye are undistinguishable, and which call their mates with stridulations which to the human ear are the same. Now, I claim that in such races as these we have the beginning of divergent species, a beginning that lies in the segregative influences of constitutional and instinctive qualities persistently inherited by the two races, though the naturalist who examines specimens of the two races can not distinguish them. All that is necessary to convert these two races into good species is the transformation of one or both of them while they are thus prevented from crossing; for we may be assured that the results of transformation under such circumstances will never be completely parallel.

Each of these races is again subdivided; for accompanying each is a diminutive form, differing somewhat in color, not so early by eight or ten days in its first appearance, producing a quite distinct stridulation, and showing no disposition to associate with the larger form. This small form was described in 1851 by Dr. Fisher as a new species under the name *Cicada cassinii*. Dr. Riley, however, hesitates to receive it as a separate species, because the differences presented by the genitalia are not constant. He says:

> There are sufficient differences to separate the two forms as distinct; but while the hooks of the large kind (*septendecim*) are quite constant in their appearances, those of the smaller kind (*cassinii*) are variable, and in some few specimens are indistinguishable from those of the large kind. This circumstance, coupled with the fact that the small kind regularly occurs with both the seventeen and thirteen year broods, would indicate it to be a dimorphic form of the larger, and only entitled to varietal rank.*

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* Bulletin No. 8, Division of Entomology, U. S. Department of Agriculture, p. 7.

I consider this case as of equal interest with the previous one; for it is an example of complete isolation between the forms of one species through diversity in their instincts. Whether these divergent instincts are sexual or social may be a matter of question; but in either case they are effectual in preventing crossing.

If future investigation shows that the small form is often produced directly from the eggs of the large form, it will have but little claim to be regarded as a separate race; but even then, if the small form breeds only with its own kind, as has been reported by several observers, and if the offspring persistently reproduce the characters of the parents, it will have to be considered something more than a dimorphic form of the large one. It would, in this case, be a dimorphic form that is assuming the character of a species. If the two forms were without segregative sexual and social instincts, then, with cross-fertility, the small form would be rapidly absorbed by the large form, which greatly preponderates in numbers; and with cross-sterility the small form would rapidly become extinct; for, through the comparative scarcity of their numbers, the representatives of the small form would have but little chance of mating with each other.

On the other hand, if the sexual and social isolation is complete, it matters but little whether the forms are mutually sterile, for the separate races or species will be protected by the positive segregation produced by the divergent instincts, even if the negative segregation depending on structural incompatibility and lack of physiological adaptation is entirely wanting. It is only when associated with positive segregation that is partial in its results that negative forms of segregation become important factors in the preservation of diverging forms.

In animals that pair, isolation through sexual and social instincts plays a similar rôle in giving preëmptive power to the males of a given species over the females of the same species that is played by potential and prepotential isolation in organisms whose fertilizing elements are distributed by wind and water. In the one case instinctive and in the other potential segregation, arising between varieties of the same species, marks these varieties as being the initial forms of divergent species.

This species presents another form of isolation which is of much interest, though it has not yet resulted in forms that can be ranked as different races. I refer to the complete cyclical segregation that exists between different broods of a given race appearing in different years. Of the thirteen-year race there are seven broods and of the seventeen-year race fourteen. As an example of different broods occurring in the same region I would mention the two broods in the District of Columbia, one appearing in 1885 and at intervals of seventeen years thereafter, and one appearing in 1894 and at intervals of seventeen years thereafter. We have no means of testing the sexual or the social instincts of these different broods, for they never appear in the same year. No one can say whether if they could be brought together they would be found as indisposed to breed with each other as are the thirteen-year and seventeen-year races. But, be that as it may, the two forms are as completely isolated as they can be, and the opportunity for independent, and, therefore, divergent, transformation, is much the same as that which exists between the thirteen-year and seventeen-year races. Two or three of the States have but one brood each; but in Ohio there are at least six seventeen-year broods, and in North Carolina one thirteen-year and six seventeen-year broods. I judge, however, from the reports that even in these last-mentioned States, there are but few places, if any, where more than three broods overlap.

I have not seen any discussion of the causes that have produced these broods, but if we may believe that they have existed for a thousand generations, a possible if not a probable cause is found in the unsettled conditions of climate that must have attended the breaking-up of the great ice period. During years of diminished cold, colonies may have taken possession of regions which were too cold for their development at the return of the seventeen-year period when the offspring should have appeared; and still some of the benumbed and delayed pupæ may have survived, making their appearance one, two, three, or more years later, when conditions were more favorable. The following observation referred to by Dr. Riley, in explanation of the accelerated or retarded appearance of sporadic individuals, throws some light on the origin of the different broods:

> That circumstances favorable or otherwise may accelerate or retard their development was accidentally proven in 1868 by Dr. E. S. Hull, of Alton, Ill., as by constructing underground flues for the purpose of forcing vegetables, he also caused the Cicadas to issue as early as the 20th of March, and at consecutive periods afterwards till May, though, strange to say, these premature individuals did not sing. They frequently appear in small numbers, and more rarely in large numbers, the year before or the year after their proper period. This is more especially the case with the thirteen-year broods.*

That climate has been an important factor in the development of the thirteen and seventeen year races is indicated by the fact that most of the districts occupied by the seventeen-year race lie north of latitude

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* Bulletin No. 8, Division of Entomology, U. S. Department of Agriculture, p. 8.

38°, and most of those occupied by the thirteen-year race lie south of that line, though in Illinois there is a thirteen-year brood as far north as latitude 40°. Dr. Riley has not referred to the coincidence, but it seems to me a fact of some interest in this connection that the southern limit of the great ice-cap which covered Canada and the northern part of the United States during the glacial epoch extended along an irregular line between the parallels of latitude 38° and 40°. Lying south of the ice region there was probably a considerable belt of country covered with pines and other conifers not adapted to the breeding of this species, so that both races, if they then existed, must have been crowded into the southern portion of the region now occupied by the thirteen-year race.

Instinctive and cyclical forms of isolation, such as cause the independent generation of the races and broods of this species, are usually associated with clearly developed specific distinctions relating to form, color, and function. This does not, however, prove that the isolative divergence was subsequent to the general divergence in other respects. The number of generations covered by the initial stage in which the different sections are only races is very small compared with those that are likely to be covered by the stages when they are separate species and genera. It is only, therefore, by rare chance that we find two forms that are still in the earliest stage of palpable divergence and are, at the same time, completely segregated by constitutional differences. Again, segregative endowments are usually developed somewhat gradually; and while the segregation is advancing other transformations take place, so that by the time all crossing has come to an end the different sections have become well-marked species. Sometimes, as in the three species of butterflies already considered, there is more or less crossing after the sections have become quite distinct species. Such cases, however, as are presented by the thirteen-year and seventeen-year races and by the different broods of this species of Cicada show that complete segregation may be produced by the psychological and physiological constitution of different races, while distinctions of form, color and manner of call are entirely wanting so far as we can observe. This has seemed impossible to some naturalists, especially since Darwin has admitted that cross-sterility can not be attributed to natural selection, and has, therefore, attributed it to the indirect effects of other qualities which have been produced by natural selection.

The great contrast in this respect between the species of Basilarchia and the thirteen-year and seventeen-year races of the periodical cicada may perhaps be partially explained by the fact that the latter spend the greater part of their existence under ground, where the conditions have not been seriously changed since the close of the last glacial period. Again, one generation of the seventeen-year race of Cicada covers many generations of the Basilarchia, bringing thirty or forty fluctuations of climate, food, etc., to the latter, while the former is, for the most part, protected from serious fluctuations.

It is of course equally impossible to prove by all inclusive observations either that transformation is never completely parallel in sections of a species that are prevented from crossing or that independent generation long continued is sure to result in independent transformation, and, therefore, in divergence; but it is of no small interest that we find in the thirteen-year and seventeen-year races of this species the strongest proof that there are sometimes divergences which our senses do not perceive. If our senses were a sufficient test, it might be maintained that between these races a high degree of local and cyclical isolation has existed for many generations, without any other form of transformation having arisen to increase the divergence; but if our informants are correct when they tell us that these races do not cross when appearing in the same district and at the same time, we need not hesitate to affirm that there must be some distinguishing characteristics by which those of one race are able to find each other, as well as segregative instincts which lead them to choose each other's society; and, even if our informants are mistaken in supposing that cross-unions do not occur, there must be some form of incompatibility between the two races, resting on divergent endowments; for otherwise we should find hybrid descendants with periods of more than thirteen and less than seventeen years' duration.

IV. CONCLUDING REMARKS.

1. *Outline of the Argument in Support of the Theory of Divergent Evolution through Cumulative Segregation.*

(1) The invariable experience of mankind in producing domestic races shows that segregation is a controlling factor. The segregation that produces domestic breeds and races is found to be of two kinds: first, that which is produced by men who designedly preserve the different styles of variation presented by one species, while at the same time they prevent them from crossing; and, second, that which commences in the indiscriminate division of the species into sections that are prevented from freely crossing through their being under the care of separate tribes of men, and which is changed into decided segregation through the diversity of selection, or of some other transforming principle, to which the different sections are sure to be

exposed; for it is found that these principles when brought to bear on separated sections never produce completely parallel effects.

(2) The paramount effects of independent generation having been shown in the broad fields of biological experiment presented by the domestication of plants and animals, the question is next raised whether species in a state of nature are subjected to influences dividing the individuals of one species into sections that are prevented from crossing; and, if they are, how far this independent generation involves segregate generation.

In my paper entitled "Divergent Evolution through Cumulative Segregation," it was shown that there are many classes of activities by which the individuals of a species are thus divided, and that, in the majority of cases, the very process that separates them assorts them into classes with reference to one or more points of character; thus producing segregation that is similar in its character to the segregation that is designedly produced by the pigeon-fancier between his various breeds of pigeons.

In the earlier half of the present paper I have shown that the planting of a small colony, resulting from migration or other causes, inevitably involves some segregation; and whenever the transforming influences of the other factors of evolution begin to operate in the different sections, this initial segregation is inevitably intensified and the divergence increased; for it is in the last degree improbable that change produced by these principles of transformation in sections that are prevented from crossing should be completely parallel in the different sections, even when exposed to the same environment.

(3) The last step is to show, as has been attempted in the latter half of the present paper, that the relations to each other of varieties, species, genera, and the higher groups are such as would necessarily be presented if all such differences were the result of evolution that is always dependent on some form of segregation, but not always on diversity of natural selection, which is produced by exposure to different environments.

We have found that persistent differences, whether varietal, specific, or generic, are not all adaptational, for some of them have no relation to utility, and that adaptational differences are not all advantageous, for some of them relate to adaptations that would meet with equal success if the organisms should exchange habitats, but that in every case divergence, whether utilitarian or non-utilitarian, whether advantageous or disadvantageous, is not maintained without independent generation.

2. *Reply to Criticism.*

In view of the examples of divergence that have been discussed in this paper, I think I may state, as in my previous paper, "It is, therefore, evident, that the simple fact of divergence in any case is not sufficient ground for assuming that the divergent form has an advantage over the type from which it diverges."* Mr. Wallace has criticized this statement,† using the following words:

> It seems to me that throughout his paper Mr. Gulick omits the consideration of the inevitable agency of natural selection, arising from the fact of only a very small proportion of the offspring produced each year possibly surviving. * * * He omits from all consideration the fact that at each step of the divergence there was necessarily selection of the fit and less fit to survive; and that if, as a fact, the two extremes have survived, and not the intermediate steps that led to one or both of them, it is a proof that *both* had an advantage over the original less specialized form.

But what if the type from which the new form diverges is surviving at the same time that the new form survives? And what if both the forms are surrounded by the same environment which they use in different ways? Where, then, is the proof that the newer form has an advantage over the older form? This was the class of facts I had been considering in the preceding paragraphs, which led to the conclusion criticized by Mr. Wallace; and instead of omitting "the consideration of the inevitable agency of selection," it was the very thing I was considering. I had pointed out that when a segregated portion of a species exposed to the same environment changes its habits, learning to appropriate resources that had not been previously used, it becomes a new intergenerating group "*in which a new and divergent form of selection is established,*" but that the result of the divergence thus produced is not necessarily advantageous, and may for many generations be somewhat disadvantageous. As I was aware that many naturalists would consider it absurd to suppose that disadvantageous or even non-advantageous instincts ever persist and become the occasion of divergent selection, I referred to Darwin's opinion that such might be the case with sexual instincts, and that the progenitors of man were deprived of their hairy coat by sexual selection that was, in its earlier stages, disadvantageous. I am not aware that Darwin has ever attempted to show how divergent sexual instincts arise and become permanently fixed as distinguishing characters of varieties and species.

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* Linnean Society's Journal, Zoölogy, vol. xx, p. 214.

† Nature, vol. xxxviii, p. 491.

"The advantage of divergence," the principle on which he relied to account for divergent habits, producing divergent natural selection, he never attempted to apply here; and, above all, when he believed the newer instincts to be either non-advantageous or disadvantageous as contrasted with the older instincts, he certainly could not have attributed advantage to the resulting divergence. As I have pointed out on previous occasions, Darwin assumed a psychological divergence in the sexual instincts of a species in order to account for the divergence in their secondary sexual characters relating to form, color, etc.; and as there is no reason given why the psychological divergence should take place, or why it should precede the change in form and color, the theory of sexual selection, as presented by Darwin, is incomplete, especially in its relations to divergent evolution. If he had thrown light on the causes of divergence in sexual instincts, he would have found the same or similar principles applicable to the explanation of divergence of all kinds. But my object in referring to his opinion here is to point out that he was free to admit that permanent divergence in sexual instincts may be non-advantageous, or even somewhat disadvantageous; and if this is true of sexual instincts, I do not see why it may not be equally true of industrial instincts. I think there is ample evidence that, when segregation has been established, divergence which is neither advantageous nor disadvantageous often arises in industrial as well as other instincts, and that these instincts may introduce new forms of environal, sexual, or social selection. The relations which exist between habits and their objects are in many species constantly varying in such a way as to constitute a series of experiments; and when independent generation exists between different sections of a species, there is nothing to prevent divergence in the results of those experiments in the different sections, even when exposed to the same environment.

In Darwin's "Posthumous Essay on Instinct," published as an appendix to Romanes's "Mental Evolution in Animals," on pages 378 to 384, mention is made of certain "imperfections and mistakes of instinct," and of certain instincts "that are carried to an injurious excess," and of others that are "small and trifling." Of the last-named he says:

> I have not rarely felt that small and trifling instincts were a greater difficulty in our theory than those which have so justly excited the wonder of mankind; for an instinct, if really of no considerable importance in the struggle for life, could not be modified or formed through natural selection.

After mentioning several which might perhaps be considered trifling but are really of great importance to the species, he alludes to a few that seem to be "mere tricks" or "habits without use to the animals." Mr. Romanes, referring to these cases, offers the following explanation on page 275 of the same work (I quote from the New York edition, Appleton & Co., 1884):

> We have seen abundant evidence that non-adaptive habits occur in individuals, and may be inherited in the race. Therefore, if from play, affection, curiosity, or even mere caprice, the animal should perform any useless kind of action habitually . . and if this habit were to become hereditary in the similarly constituted progeny, we should have a trivial or useless instinct.

As an example of a strongly inherited non-adaptive instinct in a wild creature may be mentioned the cackling of the wild hen of India after having laid an egg. This habit is referred to by Darwin as one that may be slightly detrimental; but all that is necessary to put it beyond the developing influence of natural selection is that it should fail of bringing advantage to the species; and that it is of no advantage will, I think, be generally admitted. If, then, species differ in regard to instincts that are non-advantageous, they are liable to present non-advantageous differences in form and color, resulting either from the same causes that have produced the divergent instincts, or from divergent forms of environal, sexual, and social selection produced by these instincts; it will, however, be found that segregate intergeneration is the necessary condition on which the divergence of innate characters depends.

In the present paper and in other places I have mentioned cases, representative of multitudes of others, in which there is divergence between two varieties or species occupying different districts, but surrounded by the same environment. In such cases the differences presented by the separate forms, and the divergence by which the differences have been produced, can not be regarded as advantageous; for if the forms should exchange districts, the environment being the same, no disadvantage would be experienced; and this is equally true whether the differences relate to industrial adaptations or to adaptations between the sexual instincts and the secondary sexual characters of the group, or to characters that are absolutely non-utilitarian.

Mr. Wallace says that in my previous paper he looks in vain for any proof that cumulative segregation produces cumulative divergence; but at the same time he claims that the segregation of which I speak, and which I have illustrated by a supposed case in the breeding of pigeons, is a form of selection which he calls "selection by separation." Adopting his phrase for the moment, I understand that he fully admits that in domestication "selection by separation" will produce divergence. Does he then doubt that the same process produced by natural causes will result in divergence? Or does he deny that "selection by separation" ever takes place in nature? He will probably grant that wherever natural causes act upon the representatives of a species in such a way that in each generation those presenting one style of variation are led to breed together and are prevented from breeding with other kinds, there divergence will certainly follow. This is what I call "segregation." That without it there is no cumulative divergence, and that with it there is always divergence, is amply proved by the universal experience of man in the domestication of plants and animals. All that is lacking is the consistent application of our knowledge to the theory of evolution.

Segregation is a process of much deeper significance than indiscriminate isolation, with which he seems to confound it, and one which in nature arises from a wide range of causes, some of which I have pointed out. But isolation without assortment of the forms according to any principle by which those of a kind are brought together is often transformed into segregation by the operation of the principles of transformation in the isolated sections of the species. This change is often brought about by the difference of the environments to which the organism is exposed in the isolated areas. This one form of segregation has been clearly pointed out by Darwin, though he did not recognize segregation as a necessary condition for divergence. There are, however, many other ways in which nature produces a similar result. Some of these are operative when the organism is distributed in isolated districts but surrounded by the same environment, and some of them have to do with the development of non-adaptative divergences, which can not come under the cumulative influence of natural selection.

It thus appears that independent generation coöperating with natural selection is one form of the wider principle of segregation which, in its many forms, is the ever-present condition preceding cumulative divergence. Whatever divides the representatives of a species in such a way that those of a kind are made to intergenerate while prevented from intergenerating with other kinds is a cause of segregation. This is my definition of segregation, and my theory is that whatever causes segregation causes divergence, and without segregation there is no cumulative divergence. *Now, in order to refute the theory it is necessary to show either that segregation does not take place in nature or that it is not accompanied by divergence, or that divergence takes place without segregation.* As Mr. Wallace has not attempted to prove any one of these counter propositions, I think his criticism is aside from the main issue. Even if my paper presents "a body of theoretical statements" with "no additional facts," this does not show that the theory is incorrect or the new use of the old facts unimportant in the explanation of divergent evolution. "The Origin of Species" was filled with new theories applied to old facts. The importance of cumulative divergence through cumulative segregation, if a fact, is admitted. Is it a fact? is then the question that needs to be discussed. If, however, segregation is assumed to be the isolation of sections of a species possessing exactly the same average character, the assumption will be contrary to the facts that usually exist, even in cases of indiscriminate isolation.

In the Journal of the Royal Microscopical Society, 1889, part I, pages 33-34, will be found an appreciative, though a very brief review of my theory, closing with the suggestion that fuller elucidation is needed of the alleged tendency in nature to transform separation, when long continued, into increasing segregation and divergence. Want of space in my first essay made it necessary to postpone the full discussion of this part of the theory, but in the present paper I have sought to point out some of the more manifest principles on which this general law of *intension* rests. There are undoubtedly other principles of transformation, which, when combined with separate breeding, inevitably produce divergent instead of parallel evolution; but the principles pointed out in this paper are sufficient to establish the general tendency and to show that natural selection is by no means the only principle on which the law rests. If we could obtain sections of a species presenting exactly the same average character, and if we could prevent all the principles of transformation from coming in to aid in the process, separate breeding under such conditions would perhaps never produce divergence; but, as separation never produces exactly equivalent sections, it always tends to introduce transformation, through changed or unbalanced action, and transformation in the separated sections inevitably becomes divergence. We thus gain an explanation of the fact that isolation, even when accompanied by exposure to the same environment, if long continued, always introduces divergent forms of selection. Independent generation precedes and determines the possibility of the divergence, and if it is segregative it also determines in a measure the form of the divergence; but even if it is simply separative, it involves the complete cessation of all forms of reflexive selection maintaining compatibility between the isolated sections, and, therefore, opens the way for the gradual entrance of divergent forms, first of reflexive, and then of environal selection.

3. *Construction of the Permutational Triangle.*

In my paper on "Divergent Evolution"* I referred to the permutational triangle, which I had constructed in order to determine the probability of extinction that would, under certain conditions, result from complete segregate fecundity, when unaided by any form of positive segregation. The first four lines of the table were obtained by direct observation on the permutations of letters arranged to represent the pairing of animals entirely lacking in instincts or qualities that secure the pairing together of those of one kind.

For example, let A, B, C represent three females of three varieties of pigeons, and *a*, *b*, *c* three males of the same varieties, all occupying one aviary. Now, supposing they are devoid of segregating instincts, and that they all pair, what are the probabilities concerning the pairing of the males with their own kind? These will be clearly shown by arranging the letters representing one of the sexes in one fixed order, placing the letters representing the other sex underneath in every possible permutation of order. If we make six experiments the probability is that in two cases none, in three cases one, in no case two, and in one case three, will pair with their own kind. These numbers constitute the four terms of the third line. The first, second, and fourth lines were constructed in the same way, but for the construction of the tenth line in this way I estimated that several years of constant writing would be required. The remaining lines here given were, therefore, constructed according to the following rules, which were discovered by studying the first four lines. The discussion of different methods of constructing the permutational triangle, and the interesting properties of the same when constructed, must be deferred; but I may say here that I believe it will be found an important instrument for estimating a large class of probabilities.

A	B	C
a	*b*	*c*
a	*c*	*b*
c	*a*	*b*
b	*a*	*c*
b	*c*	*a*
c	*b*	*a*

One method of constructing any line of the permutational triangle from the preceding line.—(1) Of any given line, any desired number, except the first, may be obtained by multiplying the preceding number of the preceding line by the factor of the given line and dividing the result by the figure marking the degree of correspondence of the column of the desired number. (2) The first number of any line is one less or one more than the second number of the same line, according as the factor of the line is an odd or an even number.

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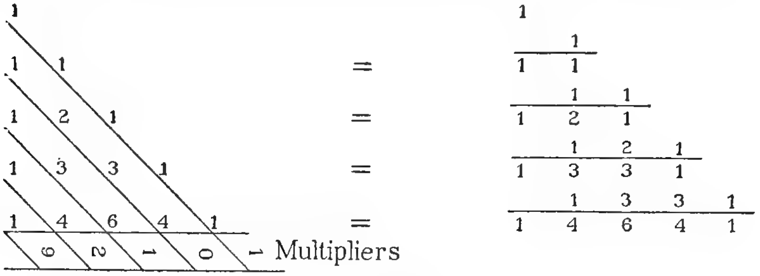
* Also see pp. 99–100 of this volume.

A method of constructing the permutational triangle from the arithmetical triangle.—Pascal's arithmetical triangle, which is the same as the table of binomial coefficients, is a series of figures, each line of which may be formed by adding the previous line to itself, as shown in the table below. Now, if we compare this arithmetical triangle with my permutational triangle we find that the first and third diagonal lines in each table are composed of the same numbers arranged in the same way. The fourth diagonal line of the permutational triangle can be obtained by multiplying each number of the arithmetical triangle by 2.



In short, by using the numbers here indicated as multipliers, each line of the arithmetical triangle may be transformed into the corresponding line of the permutational triangle. It may further be noted that these numbers by which we multiply are the occurrents standing in the first column of the permutational triangle; and these are found to be the same as the sub-factorials described by Whitworth in "Choice and Chance," Chapter IV.

The Permutational Triangle.

Factorials.			Factors.	Occurrents.	Concurrents.										
				(0)	Of the first degree. (1)	Second degree. (2)	Third degree. (3)	Fourth degree. (4)	Fifth degree. (5)	Sixth degree. (6)	Seventh degree. (7)	Eighth degree. (8)	Ninth degree. (9)	Tenth degree. (10)
				1						*The*	*ini*	*tial*	*num*	*ber.*
$\lfloor\underline{1}$= 1=	No. of *occasions*	in 1st line.	(1)	0	1					*The*	*firs*	*t li*	*ne.*	
$\lfloor\underline{2}$= 2=	„	in 2nd	(2)	1	0	1				*The*	*seco*	*nd li*	*ne.*	
$\lfloor\underline{3}$= 6=	„	„ 3rd	(3)	2	3	0	1			*The*	*thir*	*d li*	*ne.*	
$\lfloor\underline{4}$= 24=	„	„ 4th	(4)	9	8	6	0	1						
$\lfloor\underline{5}$= 120=	„	„ 5th	(5)	44	45	20	10	0	1					
$\lfloor\underline{6}$= 720=	„	„ 6th	(6)	265	264	135	40	15	0	1				
$\lfloor\underline{7}$= 5,040=	„	„ 7th	(7)	1,854	1,855	924	315	70	21	0	1			
$\lfloor\underline{8}$= 40,320=	„	„ 8th	(8)	14,833	14,832	7,420	2,464	630	112	28	0	1		
$\lfloor\underline{9}$= 362,880=	„	„ 9th	(9)	133,496	133,497	66,744	22,260	5,544	1,134	168	36	0	1	
$\lfloor\underline{10}$=3,628,800=	„	, 10th	(10)	1,334,961	1,334,960	667,485	222,480	55,650	11,088	1,890	240	45	0	1

APPENDIX III.

LETTERS PUBLISHED IN NATURE.

I. "LIKE TO LIKE"—A FUNDAMENTAL PRINCIPLE IN BIONOMICS.*

I follow Professor Lankester in the use of the term bionomics to designate the science treating of the relations of species to species. If the theory of evolution is true, bionomics should treat of the origin not only of species but of genera, and the higher groups in which the organic world now exists.

In Professor Lankester's very suggestive review of "Darwinism," by Mr. A. R. Wallace (Nature, October 10, 1889, p. 566), reference is made to "his (Mr. Wallace's) theory of the importance of the principle of 'like to like' in the segregation of varieties, and the consequent development of new species." Professor Lankester has here alluded to *a principle* which I consider *more fundamental than natural selection, in that it not only explains whatever influence natural selection has in the formation of new species, but also indicates combinations of causes that may produce new species without the aid of diversity of natural selection.* The form of like to like which Mr. Wallace discusses is "the constant preference of animals for their like, even in the case of slightly different varieties of the same species," which is considered not as an independent cause of divergence, but as producing isolation which facilitates the action of natural selection. If he had recognized this principle, which he calls selective association, as capable of producing in one phase of its action sexual and social segregation, and in another phase sexual and social selection, he would perhaps have seen that its power to produce divergence does not depend on its being aided by natural selection.

Mr. Wallace's view is very clearly expressed in the following passages, though I find other passages which lead me to think that the chief reason he does not recognize segregation as the fundamental principle in divergence is that he has not observed its relations to the principle of like to like. He says: "A great body of facts on the one hand, and some weighty arguments on the other, alike prove that specific characters have been, and could only have been, developed and fixed by natural selection because of their utility." (Darwinism, p. 142.) "Most writers on the subject consider the isolation of a portion of a species a very important factor in the formation of new species, while

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* Published in Nature, April 10, 1890.

others maintain it to be absolutely essential. This latter view has arisen from an exaggerated opinion as to the power of intercrossing to keep down any variety or incipient species and merge it in the parent stock." (Darwinism, p. 144.)

I think we shall reach a more consistent and complete apprehension of the subject by starting with *the fundamental laws of heredity,* and refusing to admit any assumption that is opposed to these principles, till sufficient reasons have been given. Laws which have been established by thousands of years of experiment in domesticating plants and animals should be, it seems to me, consistently applied to the general theory of evolution. For example, if in the case of domesticated animals, "it is only by isolation and pure breeding that any specially desired qualities can be increased by selection" (see Darwinism, p. 99), why is not the same condition equally essential in the formation of natural varieties and species? If in our experiments we find that careful *selection* of divergent variations of one stock does not result in increasingly divergent varieties *unless free crossing between the varieties is prevented,* why should it be considered an exaggeration to hold that in wild species "the power of intercrossing to keep down any variety or incipient species, and merge it in the parent stock," is the same that we have found in domestic species. Experience shows that *segregation, which is the bringing of like to like in groups that are prevented from crossing,* is the fundamental principle in the divergence of the various forms of a given stock, rather than *selection, which is like to like through the prevention of certain forms from propagating;* and I think we introduce confusion, perplexity, and a network of inconsistencies into our exposition of the subject whenever we assume that the latter is the fundamental factor, and especially when we assume that it can produce divergence without the coöperation of any cause of *segregation* dividing the forms that propagate into two or more groups of similars, or when we assume that segregation and divergence can not be produced without the aid of diverse forms of selection in the different groups. The theory of divergence through segregation states the principle through which natural selection becomes a factor promoting sometimes the stability and sometimes the transformation of types, but never producing *divergent* transformation except as it coöperates with some form of isolation in producing segregation; and it maintains that whenever variations whose ancestors have freely intergenerated are, from any combination of causes, subjected to persistent and cumulative forms of segregation, divergence more or less pronounced must be the result. The laws of heredity on which this principle rests may be given in the three following statements.

1. *The Laws of Heredity.*

(1) Unlike to unlike, or the removal of positive segregating influences, is a principle that results either in extinction through failure to propagate or in the breaking down of divergences through free crossing.

(2) Like to like, when the individuals of each intergenerating group represent the average character of the group, is a principle through which the stability of existing types is promoted.

(3) Like to like, when the individuals of each group represent other than the average character of the group, is a principle through which the transformation of types is effected.

2. *Local Segregation often Initiates Divergence, which Social, Sexual, Industrial, and Impregnational Segregation, with Corresponding Forms of Selection, Carry to Completion.*

In my paper on "Divergent Evolution" I pointed out that sexual and social instincts often conspire to subdivide a species, bringing like to like in groups that do not cross; and that in such cases there will be divergence even when there is no diversity of natural selection in the different groups, as, for example, when the different groups occupy the same area and are guided by the same habits in their use of the environment. There is reason to believe that under such circumstances divergence often arises somewhat in the following way: Local segregation of a partial nature results in some diversity of color or in some peculiar development of accessory plumes, and through the principle of social segregation which leads animals to prefer to associate with those whose appearance has become familiar to them, the variation is prevented from being submerged by intercrossing. There next arises a double process of sexual and social selection, whereby both the peculiar external character and the internal instinct that leads those thus characterized to associate together are intensified. The instinct is intensified, because any member of the community that is deficient in the desire to keep with companions of that kind will stray away and fail of breeding with the rest. This process I call social selection. The peculiarity of color or plumage is preserved and accumulated, because any individual deficient in the characteristic is less likely to succeed in pairing and leaving progeny. This latter process is sexual selection. It can hardly be questioned that both these principles are operative in producing permanent varieties and initial species; and in the circumstances I have supposed I do not see how the process can be attributed to natural selection. Varieties thus segregated may often develop divergent habits in their use of the environment, resulting in divergent forms of selection, and producing additional changes; but so long as the environment and their habits of using the environment remain unchanged, their divergences can not be due to environal selection of any kind.

Mr. Wallace's very interesting section on "Color as a Means of Recognition," taken in connection with the section on "Selective Association," already referred to, and another on "Sexual Characters due to Natural Selection," offers an explanation of "the curious fact that prominent differences of color often distinguish species otherwise very closely allied to each other" (p. 226). His exposition differs from mine in that he denies the influence of sexual selection, and attributes the whole process to natural selection, on the ground that "means of easy recognition must be of vital importance" (p. 217). The reasoning, however, seems to me to be defective, because the general necessity for means of easy recognition is taken as equivalent to the necessity for a specialization of recognition marks that shall enable the different varieties to avoid crossing. In the cases I am considering there is, however, no advantage either for the individual or the species in the separate breeding of the different varieties, and even in cases where there is such an advantage for the species (as there would be if the variety had habits enabling it to escape from competition with the parent stock, but not preventing it from crossing with the same), it does not appear how this liability to breed with the original stock can be any hindrance to the success of the individual. The significant part of the process in the development of recognition marks must be in the failure of such individuals to secure mates, which is sexual selection; or in the unwillingness of the community to tolerate the company of such, which I have called social selection.

3. *Permanent Difference in Innate Adaptations not Necessarily Advantageous Difference.*

It is often assumed by writers on evolution that permanent differences in the methods in which a life-preserving function is performed are necessarily useful differences. That this is not so may be shown by an illustration drawn from the methods of language. The general usefulness of language is most apparent, and it is certain that some of the laws of linguistic development are determined by a principle which may be called "the survival of the fittest;" but it is equally certain that all the divergences which separate languages are not useful divergences. That one race of men count by tens on their fingers and another by twenties on their fingers and toes, is not determined by differences in the environments of the races, or by any advantage derived from the difference in the methods. So, easy recognition of other members of the species is of the highest importance for every species; but difference in "recognition marks" in sections of the same variety separated in different districts of the same environment is no advantage. Under the same conditions, habits of feeding may become divergent; but, since any new habit that may be found advantageous in one district would be of equal advantage in the other district, the divergence must be attributed to some difference in the activities of the two portions of the species.

I have recently observed that, of two closely allied species of flatfish found on the coasts of Japan, one always has its eyes on the right side and the other always on the left. As either arrangement would be equally useful in the environment of either species, the divergence can not be considered advantageous.

II. UNSTABLE ADJUSTMENTS AS AFFECTED BY ISOLATION.*

In a brief passage in his volume on "Darwinism," Mr. Wallace refers to a principle which seems to me to be worthy of much wider application than he has given to it. It is a key which requires only a little filing to prepare it for unlocking some difficult problems in divergent evolution. Speaking of the infertility of crosses, he says (p. 184):

> It appears as if fertility depended on such a delicate adjustment of the male and female elements to each other that unless constantly kept up by the preservation of the most fertile individuals, sterility is always ready to arise. * * * So long as a species remains undivided, and in occupation of a continuous area, its fertility is kept up by natural selection; but the moment it becomes separated, either by geographical or selective isolation or by diversity of station or of habits, then, while each portion must be kept fertile *inter se*, there is nothing to prevent infertility arising between the two separated portions.

Here is an application of the principle of segregation (or of like to like in groups that do not cross) in which indiscriminate separation is followed by increasing divergence in the different portions, not because they are exposed to different environments, not because there is any advantage in such divergence, not because there is any need that the function should be performed more perfectly in one portion than in the other, but because intergeneration, which is the principle by which correspondence of function is secured, has been suspended for some generations; and, in the absence of intergeneration, neither natural selection, nor any other principle, is capable of preserving complete correspondence. In organisms that reproduce sexually

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* Published in Nature, May 8, 1890.

the causes of divergence are all causes of segregation; while the causes of unification, whether of functions or of structures, are causes of intergeneration. If the environments which surround the isolated portions are the same, the use of the environment, and, therefore, the forms of selection, may become divergent; if the use continues unchanged, some useless divergence in the method of securing the use may appear; or, if all the relations to the environment, whether useful or useless, remain unchanged, "the adjustment of the male and female elements to each other" are liable to become slightly divergent, producing mutual infertility, or the preference of the sexes for certain shades or arrangements of color in their mates may become slightly different, or, through some slight difference in the hereditary elements distributed in each separated portion at the first, one, or all of these causes of accumulated divergence may be introduced. I think it is evident that we have here a general principle which is as applicable to a wide range of divergences as it is to the divergence that produces mutual infertility and sterility.

The context shows that the prominent idea in Mr. Wallace's mind was divergence in the adjustment of the male and female elements, through correlation with "some diversity of form or color," resulting from divergent forms of natural selection, which had been induced by exposure to "somewhat different conditions of life." But if the reasoning is correct in the sentences I have quoted above it gives an explanation of similar divergences when the separated portions are exposed to the same environment and where there is no possible advantage to be gained by divergence. This is one of the principles I have used in the explanation of the divergences of Sandwich Island land mollusks; and I think that in the earlier stages of the development of infertility between allied forms it is often the only explanation that is applicable. It should, however, be remembered that, for divergence of this kind, it is not always necessary that the isolation should be either complete or very long continued, and that, when the forms that are not fully fertile with each other meet and more or less commingle, there is, through the very laws of propagation, without any aid from natural selection, a constant increase in the ratio of the pure breeds to the mongrels, and an accumulating intensity in the segregative instincts and the physiological incompatibilities. As this point has been fully discussed in my paper on "Divergent Evolution," I do not need to enlarge on it here.

There is, however, another phase of the subject which is indicated by Mr. Wallace's suggestion that infertility depends on "such a *delicate* adjustment" that it is more easily affected by isolation than some other adjustments. This is, I think, a very interesting point, as it suggests how it is that, in some cases at least, physiological divergence of this kind is one of the first forms of divergence that arises. But in some species other adjustments seem to be more delicate than this, and, therefore, more easily disturbed, while in others several sets of adjustments, as colors and other recognition marks with the preferences that correspond, and the habits of feeding and defense, are in a state of equilibrium, the stability or instability of which is about the same as of that which determines the relations of the male and female elements. In this last class of cases several forms of divergence may arise during the same stage of development, and that, too, when the isolated portions are exposed to the same environment. In some species a large number of characters are in a state of unstable adjustment. As Professor Lankester has suggested near the close of his review of Wallace's book, this cause of divergence seems to be specially operative in the case of human faculties. But variability with plasticity of type is not the only condition that affects the stability of segregated portions of a species. Other things being equal, a single pair of any species is much less likely to represent the average of all the characters of the species than a million pairs. This consideration throws light on the comparative lack of divergence between the land animals of England and those of Ireland, which lack has been referred to by Mr. Wallace as an objection to my theory. In this case, many millions of some of the species were probably existing in each district at the time of the separation. As Professor Lankester has pointed out, the representatives of the human species in the two districts have somewhat diverged; and the probability is that, if we were equally acquainted with the other species, we should find other examples of divergence in minor points. If the isolation is made more complete, and is longer continued, I believe the divergence will gradually become more apparent.

Mr. Wallace has mentioned another class of divergences, which he has explained as due to surplus energy in the species, ready for expenditure in ways that are not determined by conditions in the environment. I maintain that through unstable adjustment this surplus naturally takes different forms when the species is divided into isolated groups; and Wallace is content to attribute the divergence to individual variability, though each group maintains its own type. His words are:

> The enormously lengthened plumes of the bird of paradise and of the peacock must be rather injurious than beneficial in the bird's ordinary life. The fact that they have been developed to so great an extent in a few species is an indication

of such perfect adaptation to the conditions of existence, such complete success in the battle of life, that there is, in the adult male at all events, *a surplus of strength, vitality, and growth power, which is able to expand itself in this way without injury.* That such is the case is shown by the great abundance of most of the species which possess *these wonderful superfluities of plumage.* *Why, in allied species, the development of accessory plumes has taken different forms*, we are unable to say, except that it may be due to that individual variability which has served as the starting point for so much that seems to us strange in form, or fantastic in color, both in the animal and vegetable world.* (Darwinism, p. 293.)

It is no small gratification to me that Mr. Wallace has found this principle of unstable adjustment worthy of application to two important classes of divergences; and that, in the case of one of these classes, he has recognized that correspondence in such adjustments can not be continuously maintained between the isolated portions of a species. I trust that when he understands the relation in which instability and isolation stand to each other in my theory he will admit that it throws some light on the remarkable divergences of Sandwich Island land mollusks. The subject was incidentally touched upon in my paper on "Divergent Evolution through Cumulative Segregation" (see Appendix I), and more fully discussed in the supplemental paper on "Intensive Segregation" (see Appendix II).

III. INDISCRIMINATE SEPARATION, UNDER THE SAME ENVIRONMENT, A CAUSE OF DIVERGENCE.†

1. *Divergence Resulting from Isolation.*

I have accumulated a large body of facts indicating that separated fragments of a species, though exposed to the same environment, will in time become divergent. I find that, wherever a species possessing very low powers of migration is for many generations divided into a series of fragments by barriers that do not obstruct the distribution of surrounding species, more or less divergence arises in the separated portions of the species, though, in the same areas, there is no divergence in the environing species whose distribution is not obstructed. I still further find that, whenever the distances intervening between the different fragments are an approximate measure of the time and degree of separate breeding (as is frequently the case as long as the divergence does not involve any physiological and psychological segregation), these distances are also an approximate measure of the degree of divergence.

The validity of this conclusion is called in question because it is inconsistent with the theory that all divergence is due to diversity of

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* The italicizing is mine.

† Published in Nature, August 14, 1890.

selection, and that all diversity of selection is due to exposure to different environments. The divergences in the cases above referred to, it is said, are probably due to differences in the environment that are not easily recognized. This was the explanation suggested by Darwin when the facts were reported to him in 1872. The division of a species into isolated portions did not seem to him to furnish any factor that could produce divergence unless it was aided by exposure to different external conditions. The same view is expressed in his "Origin of Species," sixth edition, page 319.

My reply is twofold. (1) The theory that all divergences in Sandwich Island land mollusks are due to differences in the environment requires us to believe that there are occult influences increasing in difference with each additional mile of separation, and that these influences control the natural selection of the mollusks, but have no influence on any other species occupying the same areas. A theory that involves so heavy an assumption can not be received when a simpler theory is open to us. (2) I believe I can entirely remove this objection, urged against my conclusion on these purely theoretical grounds, by showing that there are certain causes of divergence, not depending on exposure to different environments, that are necessarily introduced by the division of a species into isolated groups; and that, under the influence of these causes, diversity of habits may arise producing diversity of selection, even while the fragments are exposed to the same environment.

I have elsewhere called attention to the fact that the independent breeding of separated groups, as far as we can judge, always tends to produce divergence; and I have shown that, when a species is indiscriminately broken into independent fragments, the tendency to divergence will, on the average, vary in direct proportion to the instability of the species and in inverse proportion to the size of the fragments; for on these factors depends the probable degree of departure of the average character of the fragment from the average character of the species previous to its being broken into fragments, and, therefore, the degree of segregation.

I wish now to show that the maintenance of certain classes of characters always belonging to an unbroken species is due to a form of selection that can continue only so long, and so far, as free crossing continues. Reflexive selection is a formative principle, depending on the relations in which the members of an intergenerating group of organisms stand to each other, while they continue to intergenerate; but when two portions of an original species have become so divergent as to compete with each other in the same area without crossing, they form incipient species, and each belongs to the environment of the other. While they are members of the same intergenerating group, their mutual influence results in reflexive selection, which maintains the correspondence with each other by which power to cross is preserved; while they are members of groups that do not cross, their mutual influence results in cumulative segregation; for it inevitably tends toward the preservation of variations that, through greater divergence, best escape from competition. I have elsewhere defined reflexive selection as being the exclusive propagation of those better fitted to the relations in which the members of the same species stand to each other, resulting from the failure to propagate of those less fitted. Among those that are equally fitted to the environment of the species, and, therefore, equally preserved by natural selection, there is often great difference in the degrees of fitness for sustaining such relations to the rest of the species as will secure an opportunity to propagate. To this class of influences belong the different forms of sexual selection through which the sexual instincts and the correlated sexual characters of the different sexes are kept in full coördination. In like manner we must believe that the pollen of any species is kept up to its full degree of potency by the constant selection which results from the failure to propagate of the individuals whose pollen is less potent or whose germs are more difficult to fertilize than the average. We call this potential selection. Again, there is a constant selection of animals that are suitably endowed with the recognition marks and calls by which the different members of the species know each other, and that have the corresponding instincts leading them to associate with their own kind. I have elsewhere called this principle of social coördination "social selection," and have classed it as a form of reflexive selection.

2. *The Cessation of Reflexive Selection between Isolated Sections Causes Divergence as Soon as Heredity Weakens.*

Independent breeding is in its very nature the *suspension*, not only of one form, but *of all forms of reflexive selection between the separated portions of the species*. The importance of the cessation of natural selection in producing the different stages of the degeneration of organs that are disappearing has been fully discussed by Professor Romanes (see Nature, vol. XLI, p. 437, and previous communications there referred to), who points out that, as the power of the special form of heredity by which any organ is produced has been built up by the many generations of natural selection that have acted on the organ, so the gradual weakening of that power follows the cessation of the natural selection. Professor Weismann seems to appeal to the same principle when he attributes the disappearance of "rudimentary organs" to the action of "panmixia." Now, in the cessation of reflexive selection which follows independent breeding, a similar principle is introduced, and the inevitable result must be the weakening of the power of heredity by which the portions of the species were held in correspondence with each other before their separation. I have elsewhere shown that separate breeding necessarily disturbs unstable adjustments; and we here see that the most stable of the adjustments by which each part of a species is kept in correspondence with every other part gradually becomes unstable under the continued influence of separation. Whenever a species is divided into two portions that do not interbreed, the forms of reflexive selection will cease to act between the two portions, and they will continue in sexual, social, and other forms of harmony with each other only in so far as the force of the old heredity holds them to the old standards. But the power of heredity in these respects will in time fail, and if the separate breeding is long continued, incompatibility in all these respects tends gradually to arise. Moreover, it is manifest that incompatibility of industrial habits involving diversity in the forms of active (or endonomic) selection will in time arise. I therefore maintain that separation, which necessarily includes cessation of reflexive selection between the portions separated, is a cause of segregation and divergence; and that this segregation is in time intensified by diversity of environal selection, through diversity in the use of the environment.

Unless the separated portions of a species possess exactly the same average character (which we must believe is seldom, if ever, the case), separation must, from the first, be more or less segregative; and even in cases where the portions completely correspond in character (if there are any such cases), *the cessation of reflexive selection which is involved in the separate breeding must result in divergence as soon as the power of heredity securing the original adjustments begins to weaken; and this is in due time followed by other forms of intensive segregation.* I therefore conclude that indiscriminate separation may be regarded as a preliminary form of segregation (that is, as demarcational segregation) and that intensive segregation coöperating with this produces complete segregation.

IV. THE UTILITY OF SPECIFIC CHARACTERS.*

I have followed the discussion on the utility of specific characters with great interest; and though I am at such a distance that my thoughts may come a little late, I wish to call attention to a few points.

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* Published in Nature, April 1, 1897.

In Nature for October 22, 1896, page 605, mention is made of a discussion on Neo-Lamarckism at the British Association. In opening the discussion, Prof. Lloyd Morgan referred to the importance of noting the bearing of certain cases that may be considered as crucial, or as nearly crucial as any that we are at present able to obtain, on the process by which specific instincts are built up. As illustrating this class of cases, he refers to the drinking instinct in newly hatched chickens, where the instinctive response begins at the point where the teaching of the parent bird would naturally be inadequate.

The question I wish to raise is whether such observations as this can do more than justify the conclusion that life-saving instincts are strengthened and established by natural selection. Are they sufficient to show that all permanently inheritable specific characters are wholly due to natural selection, or even that natural selection is always one of the factors by which any and every permanent character has been built up? It seems to me that there are large classes of facts, some of which may be found in almost every species we examine, which throw doubt upon there being any such inseparable connection between natural selection and the inheritance of characters.

1. *Right-handedness and Left-handedness.*

The majority of the human species inherit right-handedness. Does this prove that right-handedness is better for the race than left-handedness? The shells of most snails are coiled in a way that is called dextral; but some groups of species are as constantly sinistral as most groups are dextral; and of the dextral groups there are certain species that are persistently sinistral; others that are nearly equally divided between dextral and sinistral forms. Is it necessary to believe that for each species that is usually either dextral or sinistral there is some vital necessity that would exterminate, or even diminish, the species if the character was reversed? A similar class of cases is found amongst the different species of flatfish. One species persistently lies on the right side, another on the left, and I think it is Mr. Cunningham who has told the readers of Nature that there are some species in which both forms may occur. In each of these classes of cases I am unable to conceive of any advantage gained by the species that would not be equally gained if the character under discussion was reversed. *If the adaptation to the environment of a flatfish that now lies upon the right side would be equally good in case all the individuals of the species lay upon the left side, then (if I rightly understand the meaning of the terms), natural selection can not be the cause of its lying on the right side rather than the left, neither can this character of* *the species be considered a useful character, though it is persistently inherited.*

Standing near me is a flower-pot, in which are several stalks of the common calla (I believe the botanical name is *Richardia æthiopica*) in bloom; and a little inspection shows that each spathe and leaf-bud is twisted in the same way. If the leaf is held with the point up and the upper surface toward you, the half of the leaf on your left is the part that formed the inside of the leaf-bud, and the margin of the leaf on your right is the part that formed the outside of the leaf-bud. This character is quite persistent in the specimens of this species found in this city, though I am told that a leaf twisted in the opposite way sometimes appears; while in the distinct species popularly called the black calla I believe the character is reversed. Now, does this persistence prove that the character in question is essential to the welfare of the species? Are we justified in assuming that natural selection is the cause of the persistence of such characteristics? Can anyone throw light on the subject that will make it easier to believe that the adaptation of the species would be in the least impaired if all the leaves and spathes were twisted in the reverse way?

The usual method of meeting the natural inference from such cases is based on a double assumption, the first part of which is that natural selection is the only intelligible explanation of the modification of species or the persistence of character that has ever been given, and that if in any case we abandon this explanation, it is equivalent to abandoning all explanation; the second part of the assumption being that it is simply our ignorance of the facts that prevents us from recognizing the life-preserving results that are gained by the characteristic in question. This assumption ignores both the fact that species presenting characters of the kind referred to are found on every side, indeed that almost every species that fails to maintain complete symmetry of form is an example, and the fact that Darwin himself pointed out another principle besides natural selection producing persistent characters. This principle of sexual selection he carefully distinguished from natural selection, showing that the results produced by it could never be produced by natural selection, and even maintaining that "It is not surprising that a slightly injurious character should have been thus acquired." (The Descent of Man, 2d ed., p. 601.)

For my part I do not think much progress can be made in discovering where natural selection is the chief agent and where it is not the chief agent till we have carefully defined what we mean by utility and natural selection, and then adhere to our definitions. In my papers on "Divergent Evolution through Cumulative Segregation" and "Intensive Segregation" I have endeavored to show that there must be several principles somewhat similar to sexual selection, which I have grouped with it under the names reflexive segregation and reflexive selection. In the former of these papers, pages 212–214, I have pointed out that of freely crossing forms of any species it is only those that are most successful that are perpetuated; while of forms that have by isolation escaped from competition with the original stock and are not crossing with it every variation is perpetuated that is not fatally deficient in its adaptations to the environment; and this will be the case whether the forms are held apart by reflexive or environal segregation.

2. *A Difference in Use that is not a Useful Difference.*

Let us consider the case of two allied species occupying the same area, and differing from each other in what Dr. Wallace has so appropriately called their recognition marks, and in the segregating sexual and social instincts correlated with these marks. If investigation justifies the belief that an early stage of divergence, due, perhaps, to local segregation, resulted not only in sexual and social segregation, but also in what I have called divergent social selection (or what Dr. Wallace prefers to call selective association), then we are warranted in the belief that this segregative and selective principle was sufficient to perpetuate and intensify the new character, although the section of the species possessing the new character had not migrated into any new environment, and had not been exposed to any change in the old environment, and although it had not gained any new adaptation to the common environment of the two sections and, therefore, while both sections of the species were equally subject to identical forms of natural selection.

Now, seeing that the individuals of the segregated sections are able to find and keep company with associates, and in the season to pair with suitable mates, as effectually, but no more effectually, than before they were segregated, what shall we say of the usefulness of the distinctive characters that produce the segregation? It is plain that these divergent characters are in constant use; but does that prove that the divergence is a useful divergence? *Is it not possible that there should be a difference in use which is not a useful difference?* And if nothing has been gained by the difference either in maintaining the conditions of individual life, or in propagating the species, how can we call it a useful difference? And how can we attribute the divergence to natural selection, seeing that natural selection is the superior maintenance and propagation of those better adapted to maintain life under the conditions surrounding the species?

3. *Divergence through Reflexive Selection often Non-advantageous.*

I maintain that this reflexive segregation through the sexual and social instincts of the divergent sections of the species is the first in a series of divergent characters which may become a great advantage to both sections of the species by enabling them to become adapted to different kinds of resources, requiring incompatible adaptations; but it can not be claimed that the usefulness to which this segregative character may attain in the future, or may have already attained, was the cause of the divergence which was steadily perpetuated, being intensified by sexual and social selection, and so completed while as yet this character was of no service to the species. *The segregative character is preserved by its segregativeness, though at the time it arises, and for many subsequent generations, it may not be of any advantage to its possessors.* In most such cases, I believe, the initial divergence is gained by a local variety in some measure protected by local segregation; but having gained a character which secures segregation, even when commingled with the other section of the original species, it is no longer liable to be swamped by crossing. It seems to me that such cases are examples of divergence, produced by segregate breeding, brought about by sexual and social segregation, reinforced and strengthened by sexual and social selection, and not by diversity in the action of natural selection.

4. *Different Methods of Using the Same Resources not Necessarily Advantageous.*

Another fundamental distinction which needs to be kept in mind is that diversity in the action of environal selection on segregated sections of a species may be due to three classes of causes, which are the real causes of the divergence, which results in the production of different species.

(1) Different life-supporting and life-endangering conditions existing in the different districts in which the different sections of the species are distributed.

(2) Different methods of using resources and escaping dangers adopted by the different sections, though occupying the same district.

(3) Different methods of using resources and escaping dangers adopted by the different sections of the species occupying isolated districts, whose resources and dangers are alike.

If the members of the original species are brought under the influence of the first class of causes, the divergence is due to diversity in the environments to which migration introduces them; if under the second class, it is due to diversity in the action of life-preserving habits while at the beginning of the process competing with each other; if under the third class, it is due to diversity in life-preserving habits while not competing with each other.

Now, in some of the cases in the second class and in all those of the third class, it is impossible that the differences should be useful. This is most easily shown as regards the third class; for if in any case a new character attained by one of the sections is an advantage, then the same character would be an advantage for each of the other sections, exposed to the same conditions in other regions, and, therefore, there is no advantage in the difference.

If my thought is correct, some of the differences produced by diversity in the action of the several forms of reflexive segregation and selection, and all those produced by diversity in the action of environal selection, when that diversity is due to different habits that are not necessitated by any difference in the environment, are non-useful differences. Therefore, besides the principle of "correlated variation" referred to by Professor Lankester (Nature, vol. LIV, pp. 245, 365), we have other explanations of certain kinds of specific characters that are not useful; but the class of characters of which right-handedness and left-handedness are examples seem to lie beyond the reach of these explanations, and perhaps beyond the reach of the explanation suggested by Professor Lankester.

5. *Letter by T. D. A. Cockerell, with Suggestions on the Facts Mentioned Above.*

The following letter in reply to the above appeared in Nature for May 13, 1897:

THE UTILITY OF SPECIFIC CHARACTERS.

Under the above heading, in your issue of April 1, Mr. J. T. Gulick has an interesting communication, in which he asks whether it is possible to explain right-handedness, the dextral or sinistral coil of snail shells, and similar features, as having any utility of which they are certainly characteristic. Can it be due to natural selection that one snail is dextral while another is sinistral?

It is a curious fact, I think, first pointed out by Mr. Call, that in the American fresh-water shells of the genus Campeloma, *sinistral shells are more numerous among the young than among the adults.* Thus, for example, Mr. H. A. Pilsbry (Nautilus, February, 1897, p. 118), states that Miss Jennie F. Letson examined a lot of *Campeloma desisum* for him, with the result that out of 681 specimens, mainly adult, but including those from one-fourth grown up, none were sinistral. Out of 410 shells of the uterine young 3 were sinistral, slightly over 0.73 per cent." He adds: "Probably all who have collected Campelomas have noticed the greater proportion of sinistral examples among the young shells. This doubtless indicates that the reversed condition is an unfavorable one for maturition."

So here, at any rate, we have some direct evidence as to selection. I think it will strike anyone that while left-handedness might be as good for the race as right-handedness, *there is a distinct advantage in uniformity*, and that consideration alone may perhaps suffice to explain Mr. Gulick's difficulty. Among plants it may seem less obvious, but where seedlings are crowded, uniformity may save space, just as a number of objects of the same shape can usually be packed into less space than those of diverse shapes. More plants can grow in a window-box when all bend to the light than would be possible if half of them bent one way and half another.

There also occurs to me a theoretical consideration, perhaps of doubtful value. When a germ has diverse potentialities, so that it is left to germinal or environmental selection to decide which course it shall take in development, there must apparently be a certain waste of germinal energy. Any disadvantage thus arising is ordinarily much more than counterbalanced by the gain due to the adaptability of the organism, or in social species to the power of specialization of the individual for social purposes. But it may be that when no such advantage is found, there exists a small disadvantage in deviations, potential or axial, from a common standard.

What we really need, in discussing these matters, is the observation of actual facts. The facts above related as to Campeloma are worth more than any amount of theoretical considerations.

T. D. A. COCKERELL.

MESILLA, NEW MEXICO, U. S. A., *April* 21, 1897.

6. *Reply to Letter of T. D. A. Cockerell.*

The advantage in uniformity is very manifest in certain cases; and, on pages 68–70 of this volume, I refer to conditions in which it is more manifest than in the cases here suggested by Mr. Cockerell; but the advantage of uniformity does not "explain the difficulty" I have raised. For how can the advantage of uniformity explain the introduction of permanent diversity through the survival of a variation that breaks down the former uniformity, and establishes two forms where there was a single form?

The disadvantage in deviation from a common standard, if it can be shown to be a fact, is perhaps akin to the fact that variations most widely diverging from the average form are usually less fertile. But how can the advantage of a common standard cause the dividing of a species according to two different standards as in the case of some snails? For any one snail of a dextral group there may be a disadvantage in being of a sinistral form; but does that throw any light on why a species should, under one environment, divide itself into two groups, one being dextral and the other sinistral? and does it show that the process is due to natural selection? The best explanation I can suggest is given on pages 68–70.

J. T. GULICK.

APPENDIX IV.

LIST OF PAPERS ON EVOLUTION BY JOHN T. GULICK.

An article published in Nature, July 18, 1872, entitled:—

The Variation of Species as related to their Geographical Distribution, illustrated by the Achatinellinæ.

Three papers published in the Linnean Society's Journal, Zoölogy, vols. XI, XX, XXIII, as follows:

Diversity of Evolution under One Set of External Conditions, in 1872.

Divergent Evolution through Cumulative Segregation, in 1887; reproduced in the Smithsonian Report for 1891; a small portion of the same is also given in Appendix I of this volume.

Intensive Segregation, in 1889; reproduced in Appendix II of this volume.

Three articles published in the American Journal of Science for January, July, and December, 1890, as follows:

Divergent Evolution and the Darwinian Theory.

The Inconsistencies of Utilitarianism as the exclusive Theory of Evolution.

The Preservation and Accumulation of Cross-Infertility.

Four letters published in Nature, and reproduced in Appendix III of this volume.

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* See under Sexual.