SCIENCE

VOL. 81 — FRIDAY, MAY 10, 1935 — No. 2106

SCIENCE: A Weekly Journal devoted to the Advancement of Science, edited by J. MCKEEN CATTELL and published every Friday by

THE SCIENCE PRESS

New York City: Grand Central Terminal

Lancaster, Pa. — Garrison, N. Y.

Annual Subscription, $6.00 — Single Copies, 15 Cts.

SCIENCE is the official organ of the American Association for the Advancement of Science. Information regarding membership in the Association may be secured from the office of the permanent secretary, in the Smithsonian Institution Building, Washington, D. C.

WEISMANN AND HAECKEL: ONE HUNDRED YEARS[1]

By Professor A. FRANKLIN SHULL

UNIVERSITY OF MICHIGAN

THE human spirit in which there exists the spark of desire to commune with itself on any philosophical question needs only the breath of a round-numbered anniversary to fan the spark into flame. When it is blown upon by two such anniversaries, even if or perhaps particularly if from different directions, there may well be a conflagration. And when the vagaries of some organized body's activities happen to present to such a spirit the opportunity of communing with others of like mind to furnish intellectual tinder, the result would naturally be a holocaust. I give you fair warning, but trust it may not be needed. The American Society of Naturalists has agreed to devote its energies to fundamental biological matters and specifically names evolution as an example. If, when the society conferred on me the privilege and duty of making this address, it had had its eye on the calendar of the centuries, it could scarcely have failed to foresee what topic would be selected.

What form shall our commemoration of the birth of the arch selectionist and the arch genealogist take? Shall we eulogize them? That has been done recently for both in public or semi-public ways. Shall we criticize them and their views? That was done roundly in their active lifetimes in a manner which must have been regarded by them as quite ample. Shall we bring forth their chief doctrines, dust them off to give them a deceptive freshness and proceed to find in them the germ of all the essential modern views of evolution? That is much the commonest way of celebrating anniversaries. Such commendation was years ago bestowed on Weismann by an

[1] Presidential address delivered at the annual dinner of the American Society of Naturalists at Pittsburgh, December 29, 1934. Contribution from the Zoological Laboratory of the University of Michigan.

apostle who saw in the then still adolescent Mendelian principles as complete a confirmation of his theory of the structure of the germ plasm as its author could ever have coveted. I do not now recall any similarly enthusiastic appraisal of the Gastraea theory, but I would myself be inclined to accord its foundation, the biogenetic law, a higher seat at the banquet table of biological doctrines than is now the fashion to assign it.

None of these programs bids fair to lead to a correct representation of present-day thought concerning evolution. Moreover, none of them befits my temperament. I shall therefore eschew eulogy and condemnation, and refrain even from exposition of the contributions of the celebrated duo of evolutionists whose names we are now pronouncing with whatever reverence we severally feel toward them. Far more important to all of us is the present status of that branch of biological science in which they were almost pioneers. It has taken strides recently, of what length I am sure we do not all now appreciate, and I propose to use the great centenarians merely as a yardage sign beside the evolution fairway to see how far we have come. To gauge this progress involves contemplation of the historical development of certain features of the general concept.

One of the most wide-spread characteristics of life is its adaptiveness. To many naturalists fitness is the one great attribute of organisms which needs and deserves explanation. In many quarters all else is secondary. Physiology and development are made to do anything, they are strained to the breaking point, and in justification of such distortion of their principles it is pointed out that only thereby can they be made to lead to utilitarian adjustment. Logic may be cracked if through the crevice thus created fitness to the environment may be revealed. Even the facts may be made to look different by gazing at them through glasses focused on the distant adaptation.

In the mind of the average biologist, theories of evolution are made or broken according as they explain or ignore, agree with or refute the common concept of adaptiveness. The strong appeal of inheritance of acquired characters, not only to Lamarck but to modern adherents of the idea, is the easy explanation which it is believed to provide for advantageous adjustment to surroundings. The success of Darwinism was no doubt due in large measure to its obvious explanation of fitness. If it worked at all, it should explain adaptation; and it is probable that there were many who, reluctant to accept evolution itself without a *raison d'être,* did so in view of the ready solution of the adaptation problem which natural selection offered. Darwin's most ardent followers were of the opinion that all characteristics of animals and plants are useful, and were persuaded that the problem of the evolution of any given quality was solved when the service performed by that quality was pointed out. Many of the extravagances of evolution theory of the latter third of the nineteenth century—extended, I fear, into the twentieth—are directly due to this belief in the ubiquity of adaptation.

To these utilitarians the discovery of so-called mutations by DeVries must have come as a distinct shock. At least, the interpretation put upon these genetic changes by DeVries must have seemed like a sweeping away of the very rocks at the foundation of evolution. It will be remembered that most of the changes in Oenothera which the great Dutch botanist discovered were not gene mutations, and should probably not now be called mutations at all. They were changes involving chromosome arrangement and, as would be expected, affected many parts of the plant. The designation "elementary species" applied to these extensive modifications by DeVries suggested a similar origin of species in nature. When smaller changes which *were* due to changes of genes were discovered, the name mutation was naturally applied to them, and the same general significance in evolution was attributed to them despite their smallness. Thus, in the opening years of the present century some of our most eminent evolutionists were of the opinion that species arose through mutation, without necessary aid from any other process, and that natural selection was no longer an essential guide. Curiously enough, Bateson, one of the chief early discoverers of presumptive mutations in nature and later one of the greatest manipulators of mutations in genetic experiments, never saw in these changes the building stones of evolution. To his dying day, apparently, Bateson was unable to picture the formation of species as occurring through the accumulation of mutations. His rejection of them, however, had nothing to do with their usefulness. Bateson set no great store by the adaptiveness of evolution. He was even one of the great critics of the school of selectionism which flourished, and still flourishes, in his own country. His dismissal of mutations as evolutionary changes rested upon their nearly universal fertility with their parent types. How, he asked, could species, which are usually intersterile, arise from a common stock through changed individuals which were at every step fertile with one another and with their parent types? The answer to his question we are perhaps in possession of now, but it must await its turn.

The experiments of Johannsen with selection in pure lines, and those of Jennings in clones were generally regarded as confirming the conclusion that natural selection is superfluous. Why they should have been so may now seem an oddity, since the experiments as a whole were not only in harmony with natural selection but actually proved the existence of mixtures of genetic entities which is precisely the foundation on which selection must work. But even only three decades ago, to the average biologist variation was still variation. It is vain to point out, as is frequently done, that even Charles Darwin knew that some variations are inherited, others not. Nothing is more common than that a worshiper should seize upon some saying of his deity to prove that all knowledge, including that which is generally considered recent, was already his. A well-known entomologist, still living, heatedly declared that Johannsen's genes were nothing more than Darwin's gemmules, overlooking the two important facts that gemmules multiplied in the cells and were transported, neither of which things the genes do. No, with all due honor to Darwin, it can hardly now be maintained that he distinguished two classes of variations. Certainly he did not recognize a distinction based on fundamentally different origins. It is possible, moreover, to see in Darwin's admission that variations are sometimes not inherited a belief that the very same variation occurring at another time might be transmitted. Much of this early amalgamation of variation into a single phenomenon still existed in the early years of this century. Under its influence, the failure of selection experiments to produce changes in the direction of selection was regarded as another blow to the theory of natural selection.

Had evolutionists at that time looked away from the negative results of the selection experiments and looked at the positive effects—had they turned from the failure of selection within pure lines and clones and fixed their attention on the demonstration that unlike pure lines and clones exist together in populations apparently homogeneous—they would have sensed more correctly the real significance of those experiments, and would have reversed their conclusions regarding the effectiveness of selection. A glimpse of what might have been deduced from the pure line and clone experiments was afforded by the experiments of Castle on hooded rats. The sorting, sifting action of selection was there fortunately seen at work upon the only kind of variation which can lead to evolution. Mendelism was, moreover, older by that time. Variation of a quantitative and apparently continuous type was soon thereafter seen to be as truly Mendelian as the simple sharply defined steps. Many intricacies of gene interrelationships were revealed, and the Mendelian system, which in the early years after the 1900 discovery was freely stigmatized as too simple to be true, was now growing too complex to be true.

It is ofttimes now regarded as strange that the new knowledge of genetics did not earlier influence evolution theory. Every writer discussing the general field of evolution recognized that transformations of species involved heredity, and every such writer described the simple genetic processes and the mechanism on which they rest. But for many years not one of them attempted to show even approximately how evolution must proceed as a consequence of the operations of that mechanism. In explanation of this neglect it need hardly be pointed out that a mathematical mind and training are prime requisites to delving into the evolutionary processes dependent thereon. Fortunately, these essentials are now provided in company with masterful attainments in the purely biological field, and at the hands of Wright, Fisher and Haldane we are gradually being shown what the course of evolution must be in the light of the Mendelian mechanism. We have learned what may happen to gene ratios without any particular cause; what should follow any definite schedule of mutation, particularly of repeated mutation; how migration affects the genic composition of a species; what consequences must flow from any selective advantage or disadvantage of any gene or collection of genes; in what manner the expected results are modified by the size of the population; and the very considerable differences in some of these influences depending on whether the population is growing, stationary or declining. It is already plain that there is much in evolution which most of us had not heretofore suspected.

Let us pause to congratulate ourselves upon our accomplishments. I proposed a moment ago to use the great evolutionists born a century ago and actively championing evolution and its supposed factors half a century ago as distance signs to measure our progress. Having taken our drive and located the evolution ball approximately in its present lie, let us pace off the distance beyond our markers. We find Haeckel tracing pedigrees, and not greatly concerned with causes. Weismann, firmly convinced of the correctness of the selection doctrine, was applying it to a wide range of animal characteristics. Indeed, it was to him universally applicable, since all qualities were apparently held useful. In furtherance of their individual fortunes, animals were held to have resorted to all sorts of ingenious devices—almost as ingenious as the theories of the evolutionists who were capable of detecting them. Their colors and shapes changed to render them inconspicuous to man, no questions being asked about their visibility to their real enemies. Ornaments arose in them in response to the love of beauty in one sex, when no other evidence of the esthetic sense existed. Strikingly gaudy patterns and blatantly obvious shapes sprang up to proclaim from the housetops with clarion silence the possession of a disagreeable taste or means of attack which ofttimes was not, from any other source than the warning, known to exist. Many a species was held to have taken advantage of these danger signals to steal an unearned immunity from the predatory world by imitating those which gained a freedom from attack by direct methods. To this time also belongs the discovery of the defenseless animals whose mean individual psychological attainments entitled them to the once common designation "bromides," and which in keeping with these qualities invented the modern game of "follow the leader," and developed conspicuous marks on their hinder parts. To the spirit of that time, even if later in actual years, belong also the bogey colors, and we find it seriously proposed even in the latest edition of one of the great cyclopedias that a two-inch fulgorid bug owes its particular color to the advantage of resembling a crocodile. But I must end this recital of examples, lest you suspect I have inadvertently confused my dates by a few months and that it is really the centennial of Mark Twain which we are celebrating.

Truly we have come a long way. I fear, however, that the spirits of the preceding generation of evolutionists must be disappointed in us. We have progressed much more slowly than they evidently expected we would, and have taken a very different road. For Romanes, writing in the early nineties of the last century, shortly before his death, and advocating not only the Darwinian selection but the Darwinian inheritance of acquired characters as well, expressed the firm conviction that another ten years would see all outstanding difficulties in the way of evolution theory removed, and an era of good feeling inaugurated in which all evolutionists would be of like mind. This forecast reminds one of that other justly famous prediction of an artificial basic evolution, a wager laid at the turn of the century between an eminent physiological chemist and a celebrated cytologist, the stake being the best hat in New York City, that protoplasm would be created in the laboratory within ten years. Again we have failed in what was expected of us. It seems that in biology even Ten Year Plans have a habit of lagging behind schedule.

In view of the great expectations indulged in by biologists of a few decades ago, perhaps we owe ourselves a measure of justification. Is not our slowness really a consequence of our predecessors' speed? Have we not had to clear away endless corduroy, running crosswise and leading nowhere, before we could build the permanent pavement in a forward direction? Is there not even now a great deal of energy spent in hewing logs to repair the corduroy which might be spent in mixing concrete for the new highway? It would not be difficult to maintain that our present views of evolution would be sounder if there had been no direct study of it—certainly if there had been no speculation upon it—from the publication of "The Origin of Species" down to 1910 or even 1920. This is probably true of many great developments. The historical order is not the logical nor the economical one. The foundation facts on which a correct evolution doctrine must rest would have been sought—were sought—more for their bearing on physiology, genetics and embryonic development than for their relation to evolution. Hence the absence of evolution speculation would have removed no stimulus necessary to progress toward a correct solution of evolution problems.

These comments are made, not with any belief that the rugged individualism of science by which any one was free to follow any whim and propose any theory could have been replaced by a new deal wherein only directed effort would be permitted, but only to explain our delay in arriving at sound results. It was inevitable that easy speculation should have been preferred to experimental search for principles. Little else than speculation was at the foundation of the theories of warning color, mimicry and signal colors, for example. Supposed evidence for them of an observational sort was garnered from hither and yon with all the nonchalance of the smoker of a well-advertised brand of cigarettes. The colors of animals are no more marvelous if left unexplained than are the theories advanced to account for them. They are no more wonderful than is the ingenuity of man in explaining them. If we could explain the evolution of the human imagination we would have a better understanding of the theories named than we can get now.

The danger from most theories is the heavy hand they lay on subsequent workers. Fisher, one of the leading exponents of the new approach to natural selection, refers to mimicry as "the greatest post-Darwinian application of natural selection." This remark is the reason for my perhaps unwarranted attention to these theories of color. Its truth or error probably hinges on the meaning of one word in it. The saving or damning ambiguity of the word "greatest" is that it may refer to magnitude measured in decibels rather than in pounds. I do not know the meaning attached to it by the author of the statement. I am reluctant to think that his valuation may be only an example of nationalism in science, though I can scarcely imagine it coming from a leader of an important modern biological movement in any intellectual country but one. I often wonder what scientific foibles we subscribe to in America because of a magnetic personality, powerful leadership or affable volubility. There must be some.

What does one do with a misapplied theory? Biologists have answered variously. The biogenetic law has been completely rejected in some quarters because the specific events which it was used to explain were erroneously chosen. Even those who reject it admit the correctness of a modified form of the theory. One of Mendel's laws was found to be violated by linkage. But was it rejected *in toto*? No, it was modified to include all chromosome behavior. Natural selection, at the end of the last century, was judged—and still is judged by some—from the applications of it made by its supporters, and was by many able biologists rejected. The trouble with the natural selection theory is not that it will not work, but that it will not accomplish the results attributed to it. The germ theory of disease does not fall down when a mistake is made concerning the identity of the causative agent of a particular malady. It is even possible that the Nobel prize in medicine might be awarded for a discovery which proved later to be an error. What theory—what valid theory—is there that has escaped this fate of wrong application?

Merely to use a great principle to wrong ends is the simplest and least harmful of the untoward events that can happen to it. Such a principle might even be distorted to a considerable degree and still be worth rescuing, rehabilitating and recognizing by name. It is already evident that this is to be the destiny of natural selection. There are still some to whom natural selection means the explanation of a host of supposedly advantageous small characters which was the occupation of Darwinian supporters of a generation ago, some of whom still live. To these few, the word "selectionists" is still used to mean essentially the explainers of animal colors. It is a hopeful sign, however, that capable biologists have been able to approach the whole question of selection again in a semi-abstract form with no particular qualities in mind as needing, above all things else, an explanation. If architectural details can be forgotten for a time while sound plans dealing only with stresses and strains and strength and resistance of materials are evolved, it is likely that we may emerge with a practical and at the same time harmonious edifice. We may thus acquire a doctrine which, unlike the portmanteau theory derided by Yves Delage as capable of yielding up only what was put into it, will resemble more the magician's hat or the widow's cruse in dispensing far more than was first assembled in it—will indeed bring forth more than hopeful enthusiasm ever imagined it to contain. But this will not happen in ten years.

Having thus congratulated ourselves upon the magnificent distance of our drive, let us return to address the ball for the next stroke. Let it be borne in mind that our present position is not the result of a second shot starting from mimicry, sexual selection and similar concrete proposals. That ball was lost. Our recent drive started afresh from an alternative tee, namely, genetic phenomena. The club used is fashioned along fundamental Mendelian lines. We recognize that evolution consists of changes in the nature or arrangement of genetic units. These units are with few exceptions chromosomally contained, the known exceptions being certain plastid characters. A certain influence of cytoplasm upon early development has often been hailed as evidence that fundamental race characteristics are determined by the general protoplasm, but there are several indications that even this cytoplasmic influence comes under the control of genes within a generation. The genes in bisexual animals recombine in a fairly free way every generation. The restrictions imposed upon this recombination by inclusion of many genes in a single chromosome are rapidly removed by crossing over, so that in a long-time project like evolution they may be ignored. The genes may change, and change again, and return to any of their former states. Since evolution deals with populations, migration into and out of any group may change its composition. Relative proportions of the alternative genes in a collection of individuals determine the nature of the population, and these proportions are modified by the accidents of recombination, accidents of survival, changes in the genes and the accidental wanderings of individuals. If any gene or combination of genes confers an advantage that is expressed in increased relative numbers of descendants—and no other advantage is an advantage in evolution—that gene or combination gains over its alternates. A gene in one setting of accompanying genes and environment may have one effect, but in another setting a very different effect. The interplay of all these factors results in evolution so far as it depends on the regular mechanism of Mendelian heredity.

Using these fundamental features of the evolution mechanism Wright, Fisher and Haldane have formulated the expected consequences of each factor under various suppositions. They have postulated mutation rates, including reverse mutations, migration rates, selective advantages and various population sizes, and out of them have pictured the evolution process in the abstract. Along with this service they have performed two others of which they may not have been aware. Their mathematical treatment has served to take evolutionists out of themselves, to make them less introspective, to force them to look for factors of evolution outside of their own minds, which is where most of them have been looking heretofore. It has also helped to develop an inferiority complex where one was badly needed but never before existed. While their mathematical discussions are frequently summarized in plain language, there are many parts of them which impress a non-mathematical person with his own incapacities. They show that many means of acquiring a valid opinion are closed to such a person.

How immensely valuable it would have been to the whole structure of evolution theory to have had such treatises circulated among naturalists just when the theories of animal coloration, for example, were being promulgated! How our friends the economists and psychologists must envy us now the possession of one small means of reducing the number of those who feel qualified to speak!

The debt we owe to our mathematical-minded friends is obvious. Any one who acknowledges that two and two make four should recognize this obligation, even if he does not follow their reasoning. So great is our debt to them that it would be ungrateful not to point out any shortcomings we think we see in the purely biological assumptions they make. It was Johannsen, I believe, who adjured us to treat our biology not *as* mathematics, but *with* mathematics. None of these leaders is under the illusion that statistical methods alone will solve all evolution problems, but it is easy to argue from mistaken premises. This I think at least one of them has done.

An error of a purely biological sort I deem to have been made by Fisher relative to the direction of mutation. If mutation is the beginning of every evolutionary change, obviously evolution can not proceed in a direction in which no gene changes. Fisher plainly assumes that mutation is purely random with respect to direction. When he merely states that mutation is random, it would be possible to suppose that he means fortuitous as to time or locus. This can not be all that he does mean, however, for his philosophy of evolution requires in several respects that mutation be random as to quality as well. Ford, who has been associated with Fisher in some evolutionary projects, and who apparently takes his statistical cue from the latter, is more specific, and claims explicitly that mutation is purely fortuitous in quality (that is, in the nature or direction of the changes) as well as in locus. It would be easy to imagine that support for this assumption has been given by competent geneticists when really they offer no such corroboration. Muller, for example, points out that mutation is random, but means thereby only that it is non-adaptive, that its nature is not determined by the environment. Fisher's assumption clearly is that mutation is happening, not just in every *possible* way (the possibilities being limited by the structure of the genes), but in every *conceivable* way. He holds that mutation provides *every* avenue of progress and that something chooses among the radiating paths. That thing he holds, as do we all with less sweeping premises, to be natural selection. Whether his belief in the randomness of direction of mutation has led him to his faith in the Allmacht of selection or whether his conviction that selection is all-powerful moved him to conclude that mutation must be random in quality is uncertain. The two are closely bound, and their adoption by Fisher constitutes, in my opinion, one of the weaknesses of his position.

There are many reasons to conclude that mutation is not random in quality, but is directed. This does not mean that a mutation occurring at a particular time and place must be of only one sort, though it is conceivable that even this might be true. Still less does it mean that successive mutations at the same locus are likely to go farther and farther in the same direction, though even this has been held probable by at least one geneticist. It means merely that some of the conceivable paths, probably most of them, indeed, are closed. The repeated occurrence of certain mutations, like that to white eye in Drosophila, is an indication of such guidance. So is the production of parallel mutations in related species, as the occurrence of ruby eye and a number of other mutations in two species of Drosophila or a number of color mutations in mice, rats, rabbits and guinea pigs. It strains one's faith in the laws of chance to imagine that identical changes should crop out again and again if the possibilities are endless and the probabilities equal. Reverse mutations would be very unlikely if the direction of mutation were purely random. Were eye color mutations random in quality, every color in the rainbow should be represented. The fact that in Drosophila many shades of red have arisen, while not once has there been a mutation to green or blue, leads to a suspicion that for some reason these latter colors are impossible. All this limitation is rendered *a priori* very probable by the fact that genes must be chemical entities, and that no chemical substance is capable of reacting in every conceivable way. To assert, as Fisher does, that mutation has nothing to do with the direction of evolution is like assuming that a tetrahedron may fall, at different times, with ten or a hundred points uppermost. The ten points and ten opposite sides to fall upon do not exist. How great a restriction is placed upon the course of evolution by the inability of genes to mutate in certain ways it is impossible to tell; but it may easily be much greater than any of us suppose.

A logical consequence of the belief that mutation is wholly random in quality is the conclusion that species change promptly and perhaps rapidly in that direction in which their own best interests lie. If mutations really do occur in every conceivable direction with equal probability, and some of them confer advantages, there can be no reason why a species should not start at once in one or more of the favorable directions, at a speed dependent on the frequency of mutations in those directions and the degree of advantage afforded by them. Thus, a species should at any moment be about perfectly adapted to its environment. And, indeed, we are told that this is what we should expect. Alas! When I reflect that, under a physician's orders, I must forever refrain from the delectabilities of apple pie, I am reluctant to believe that organisms are as well adapted as they might conceivably be. And if I am reminded that the defect which I have cited is that of an individual, not of a species, I need only add that if I were making a human race perfectly adapted to its environment I should certainly wish to endow it with an enzyme that would digest cellulose. It seems clear to me that species are not, probably in any instance, as well adapted to their environments as they could be. They may be approaching as close an adaptation as is permitted by the mutations arising in them, but that must fall far short of perfection. For every living kind this best of all possible worlds must yet have room for improvement.

Fisher has adopted views of the origin of and reason for dominance with which Wright and Haldane are unable to agree. In so far as his opinion rests on the assumption that genes produce different effects, depending on the company they keep, it is well enough grounded. But the smooth working of the scheme of growing dominance demands again a steady flow of random—qualitatively random—mutations. The mere fact that wild type genes are so generally dominant over their mutants indicates that, if Fisher's theory of becoming dominant through accumulation of accessory genes which increase dominance be correct, this accumulation must occur relatively rapidly. That is, genes of the right kind must always be quick to appear, no matter what is demanded of them. This could only happen if genes of every conceivable kind were appearing with what must be considered, in evolution, great frequency and regularity.

This concept of gradually changing dominance is probably responsible, at least in part, also for Fisher's sliding scale of gene effects. He states that if a change of 1 mm in some quality has selective value, a change of .1 mm in the same quality and in the same direction will have approximately one tenth as great selective value. When I read this statement I recall that I, as a boy at the county fair, strove with mighty blows to lift the heavy weight until it rang the bell, but never succeeded. I could get three fourths or even nine tenths of the way. Had I held Fisher's philosophy, I should have demanded three fourths of the Negro doll which was the reward of success; but I would have been denied. In living things, just as in carnivals, there are thresholds which must be reached before any effect is produced. The new philosophy of natural selection has not abolished them. They exist in development, in general physiological processes, and I doubt not in adaptation.

We have here a group of more or less related situations in which a wrong reading of biological facts may easily lead to wrong conclusions, despite the most careful of mathematical calculations. I yield to no one in my satisfaction in the progress recently made in attacking evolution over the mathematical route. But we should be exceedingly careful to base the calculations upon sound biology.

At still another point on the new battle front is there need of consolidating our positions. In the late war, when an official bulletin described the activities of the military as a consolidation of its gains, it meant that the army had retreated. Perhaps that is what is needed in the present evolution skirmish, at least in certain places. The consolidation is needed in our attitude toward the origin of those qualities which have no value. I know that I shall be challenged concerning what I am about to say, but I do not entertain any doubt whatever that living things are possessed of characteristics that are of not the slightest use. In an ordinary assembly I might defend this position by illustrating it only from mankind, and asking my hearers merely to look about them for examples. Before the American Society of Naturalists, however, it seems necessary to go afield and refer to species in general.

Most systematic workers appear to be convinced, at least with respect to the groups with which they are familiar, that the differences between nearly allied species are chiefly useless distinctions. Students of animal color, particularly of insect color, should take notice. They are prone to claim a use for specific distinctions in color; in view of the apparent non-adaptiveness of other species differences, however, it is far safer to acknowledge usefulness of color only after the most complete proof of it has been obtained.

It is these useless characters which constitute one of the puzzles of evolution. They are a particularly heavy load upon the natural selection doctrine. Nor are specific characters the only ones that fall in the seemingly non-adaptive class. Many great evolutionary developments in the past give every indication of having been without advantage, such as the curious armatures of some of the huge mesozoic reptiles and some of the extinct mammals. So numerous are the apparently useless characters of organisms and the ostensibly non-adaptive changes in them that most evolutionists have felt obliged, at one time or another, to postulate some other factor besides natural selection to account for them. Could such a factor be discovered and be proved general, most of the outstanding problems of evolution would be started on the way to solution. What the world most needs, then, is not a good five-cent cigar, but a workable—and correct—theory of orthogenesis.

Unfortunately the Lamarckian principle that the need of or desire for a thing helped to bring about its development does not apply to biological theories any more than to animal characteristics, and no acceptable theory to account for wide-spread non-adaptive evolution has ever been devised. Of the leaders of the statistical movement in the study of evolution, only Fisher seems oblivious to the need of such a principle, perhaps because he recognizes only a very small minimum of useless qualities. Wright is fully cognizant of the abundance of non-adaptive characters, and allows accident to explain the smaller examples, up to the level of varietal or even specific differences. He is aware, too, that much more than this is needed. Haldane is conscious of his possible ignorance in this small field of evolution inquiry, namely, the adaptiveness or non-adaptiveness of specific differences, but has made a brief but serious attempt to give an explanation to orthogenesis. He suggests that the genes producing the useless adult character may have a selective advantage in the embryo. Certainly no general theory of evolution can go unchallenged which does not permit the origin of unadaptive characters. I wonder whether the mathematical possibilities of non-adaptive evolution have been as thoroughly explored as they may be. I trust that the ray of hope which formulas, curves and equations have given us has not emitted its last flicker in this particular direction.

While waiting for possible further developments in the statistical field we need not stand idle. Some of the most significant of evolutionary changes appear at present not to be amenable to mathematical study. Their exemption from statistical formulation derives first from their infrequent occurrence (and statistics is ever based on considerable numbers, so that random opposite effects may tend to cancel one another) and second from the uncertainty whether they are wholly accidental. To shorten the discussion I shall pass by, despite their importance, the very quick transitions from one species to another, not through gene mutation and shifting of gene ratios, but by polyploidy, discovered so much more abundantly in plants than in animals. I shall likewise omit consideration of interspecific hybridization as a means of attaining recombination of genes.

It is rather to the isolation of species from one another that I shall turn for what seems to me some of the most significant of recent advances. For isolation has been in the past as far from a satisfactory explanation as any other major phase of evolution, excepting only non-adaptive modification. Though geographic isolation was first in the minds of evolutionists who realized the importance of insularity of groups in the development of differences between them, it has played little part in the new forward strides toward a knowledge of the segregation of species. It seems now a little odd that geographic separation ever should have been relied on to produce so many of the differences that were observed to exist between closely allied species. True, it aided each group in experiencing a different series of shifts of gene ratios, and could easily have brought about the visible distinctions between species. What it could not do, in accord with anything then known of heredity, was to produce the sterility, partial or complete, which nearly always arose between such groups along with their visible differences. This sterility was not lightly to be dismissed. So characteristic of species is their sterility with other species that the late Professor Bateson was ready, as already pointed out, to reject mutations as the building stones of evolution because every known mutant could be crossed with its parent type with resultant fertile progeny. How could intersterile species arise out of interfertile mutations? It was of course conceivable that differing aggregations of genes would entail a reduction of fertility if brought together. Something is known to-day of combinations of genes that induce sterility between types, but these are genes whose only known effect is that upon fertility, and it is combinations of these particular genes, not combinations of general gene complexes, which cause incompatibility of gametes or infertility of zygotes. But even if there had been some plausibility in the assumption that accumulation of gene differences of any sorts whatever would gradually lead to intersterility, evolutionists of the period to which we are looking back should have been cautious in attributing sterility to geographic isolation, for they found the same sterility to exist between types for which there was no apparent reason for geographic separation. They frequently took refuge in the belief that geographic isolation existed where none could be seen; but imagining barriers where none was apparent was as objectionable a procedure as hypothecating anything else merely to save a theory.

Although a master key to the problem of interspecific sterility has not been found, at least one individual solution and several clues have been discovered, none of which bear any relation to environment. Geographic barriers may exist, but they are not necessary to the separation of taxonomic entities. And the search is rightly being made among genetic phenomena and their related cytological events.

Only a little while ago there was a strong hope that abundant sources of intersterility would be found in the phenomena of meiosis, knowledge of which is itself but little more than a generation old. Organisms have solved the problem of approximate stability of type, coupled with a degree of genetic plasticity, by adopting, along with gamic reproduction, the synapsis of homologous chromosomes followed by their regular separation in the formation of the gametes. This method insures the viability of by far the majority of all combinations, in place of the chaos and excessive mortality which must occur in the absence of any such scheme. Yet it provides slow change through random recombination of chromosomes as groups, and fairly rapid reconstitution of individual chromosomes through crossing over.

Into this mechanism there creep occasionally such changes as inversions, duplications and translocations—rearrangements of genetic material without any necessary changes in its units. These irregularities were eagerly studied in the search for causes of intersterility. For, since the rapprochement of homologous chromosomes in each generation is apparently due in large measure to the similarity of the genes they contain and of the arrangement of those genes in the chromosome, the occasional changes in this arrangement just referred to might reasonably be expected to prevent much of the usual synapsis, with consequent irregularities of meiosis, and deficiencies or surpluses of genes in the several gametes. Some loss of fertility would naturally follow each such irregular event. It was conceivable, however, that among the products of the irregularity two similarly disarranged chromosomes might have the good fortune to meet in fertilization, along with the usual (or some other viable) combination of the remaining chromosomes, and a new type to be the result. Such a type might differ little or not at all from the original, yet it seemed plausible that there should be a degree of infertility of their hybrids because of the unmatched constitution of their chromosomes.

I speak of these discoveries in the past tense and subjunctive mood because there is now considerable doubt of the efficacy of the disarrangements of chromosome parts. The only well-known species in nature differing chiefly by an inversion are two species of Drosophila, and though their hybrid is sterile as expected, that sterility is evidenced by degeneracy of the reproductive system at a time too early for synapsis. Likewise, the best known translocations have not led to sterility of hybrids. The outlook for an explanation of intersterility as a consequence of chromosome aberrations is thus somewhat dimmed, though it can hardly be said that the possibilities have been explored and the method should not be abandoned as useless until more instances of its inadequacy are known.

No great despondency need descend upon us, however, because of the failure of such obviously possible explanations of intersterility to meet our early expectations. We have left to us the sterility genes which have been most carefully studied in various relations within species. All that is needed is to extend these relations to crosses between species, and to postulate dominant complementary genes, each existing harmlessly in one species but blocking some essential reproductive process when together with another in the same individual, as in the species hybrid.

Regardless of the nature of the cause of sterility of hybrids, once such a mechanism is in existence in two individuals or groups of individuals, all that is necessary thereafter is that different mutations shall occur in the two types—mutations which can not be transferred from one to the other by hybridization—and two species are distinguishable. These things are well known, I think, to all of you; but their significance has not yet crept into the consciousness of the evolution fraternity in general. Their possibilities with reference to the isolation of species are endless. Moreover, so spontaneous may they be that sterility between types may spring up anywhere. No longer do we need to postulate a considerable divergence of types before intersterility arises. Sterility may originate early in the process of separation, or even before any other modification commences. It may be and probably is one of the primary reasons for the splitting of species, since any changes that do arise by mutation or otherwise are thereby removed from some of the leveling influence of hybridization. If this surmise is correct there may be hosts of incipient species about us, differing in no observable respect from other members of what is still called their species, but possessing already the quality which renders them incapable of breeding with certain of their fellows. Whether these partially isolated groups survive the accidents of elimination, the chances of breeding with those with which they still are fertile and other factors of preservation are other questions which may now be regarded as secondary.

We have arrived at our destination, namely, the present-day concept of evolution. At least we have approached as near that goal as the guide is licensed to conduct parties. We have traveled laboriously, and naturally look back upon the distance traversed with satisfaction. We may assume a supercilious attitude toward our predecessors, and view their evolutionary ideas with scorn. Their theories may seem to us conceived in romanticism, and their arguments to be a cobweb of irrationality. In the words of a popular writer, on whom I tried out the general drift of this address before bringing it to you, we may regard their period as one of bewilderingly obfuscatious scientific hallucination, abbreviated in this day of governmental alphabetics to BOSH. But even though this judgment were correct it would little behoove us to harbor it. Far more important than to congratulate ourselves upon our accomplishments is to acknowledge how much is still undone. While I am quite unwilling to share with Osborn, Barbour and some others the view that we are still as ignorant of the factors of evolution as biologists were a generation ago—a few biologists may still be—I am quite certain that even a moderately full knowledge of them is still far beyond. Even were the only outstanding difficulty the existence of non-adaptive qualities in organisms we should be still far from finality; but this I regard as the heaviest task before us. The alternative of this task, which has sometimes been proposed, namely, a denial that any evolution is non-adaptive, is not to be considered until every other possibility has been thoroughly explored. For most of us a time which is ripe for such denial will never come, for the necessary explorations of other leads can not possibly be made in many times ten years.

SCIENTIFIC EVENTS

THE TWENTY-FIFTH ANNIVERSARY OF THE BROOKLYN BOTANIC GARDEN

INVITATIONS and announcements have been issued for the celebration of the twenty-fifth anniversary of the Brooklyn Botanic Garden from Monday to Thursday, May 13 to 16. The programs fall under four headings—civic, social, scientific and educational.

On Monday evening the president of the board of trustees, Edward C. Blum, will preside. The speakers include the president of the borough of Brooklyn, the Honorable Raymond V. Ingersoll; the commissioner of parks, the Honorable Robert Moses; the president of the board of education, the Honorable George J. Ryan, and the chairman of the Botanic Garden governing committee, Miss Hilda Loines. The principal address will be given by Dr. Albert F. Woods, director of the Graduate School, U. S. Department of Agriculture. The program will be followed by a reception and inspection of exhibits illustrating the progress of development of the Botanic Garden since 1910. A feature of this exhibit of special scientific interest will be a selection of some of the incunabula and other rare books and manuscripts in the Botanic Garden lbrary.

On Tuesday afternoon the twenty-first annual spring inspection of the garden, with the Honorable Fiorello H. La Guardia, mayor of New York, as guest of honor, will be held. This will be in charge of the woman's auxiliary of the garden.

The scientific programs deal with the progress of various aspects of botanical science during the past twenty-five years, as follows:

Wednesday Morning: Presiding, Professor R. A. Harper, Columbia University.

(1) "Virus Diseases of Plants: Twenty-five Years of Progress, 1910–1935." Dr. L. O. Kunkel, Rockefeller Institute.

(2) "Twenty-five Years of Cytology, 1910–1935." Professor Charles E. Allen, University of Wisconsin.

(3) "Twenty-five Years of Genetics, 1910–1935." Dr. Albert F. Blakeslee, Carnegie Institution of Washington.

Wednesday Afternoon: Presiding, Professor Edmund W. Sinnott, Barnard College.

(1) "Twenty-five Years of Plant Physiology, 1910–1935." Professor Rodney H. True, University of Pennsylvania.

(2) "Light on Vegetation, 1910–1935." Dr. John M. Arthur, Boyce Thompson Institute for Plant Research.

(3) "Twenty-five Years of Ecology, 1910–1935." Dr. H. A. Gleason, New York Botanical Garden.

(4) "Twenty-five Years of Forestry, 1910–1935." Dean Samuel N. Spring, New York State College of Forestry, Syracuse University.

Wednesday Evening: Presiding, Dr. William Crocker, Boyce Thompson Institute for Plant Research.

(1) "Twenty-five Years of Plant Pathology, 1910–1935." Professor L. R. Jones, University of Wisconsin.

(2) "Twenty-five Years of Systematic Botany, 1910–1935." Dr. Elmer D. Merrill, New York Botanical Garden.

(3) "Twenty-five Years of Paleobotany, 1910–1935." Dr. G. R. Wieland, Carnegie Institution of Washington.

(4) Motion picture (silent)—"The Life Cycle of a Fern." Harvard film. Premier showing.

Thursday morning will be devoted to a horticultural program, with John C. Wister, director of the Arthur Hoyt Scott Horticultural Foundation, Philadelphia, presiding. The papers are as follows:

(1) "Twenty-five Years of Horticultural Progress, with Special Reference to Foreign Plant Introduction, 1910–1935." Dr. W. E. Whitehouse, U. S. Department of Agriculture.

(2) "Opportunities for Women in Horticulture, 1910–1935." Dr. Kate Barratt, the Swanley (England) Horticultural College.

(3) "Growing Plants in Sand with the Aid of Nutrient Solutions: With Special Reference to Practical Applications." Professor C. H. Connors, Rutgers University.

(4) "Modern Methods of Plant Propagation." Dr. P. W. Zimmerman, Boyce Thompson Institute for Plant Research.

(5) "Plant Patents." Colonel Robert Starr Allyn, deputy commissioner of sanitation, New York City.

(6) Motion picture—"Naturalized Plant Immigrants." U. S. Department of Agriculture, Bureau of Plant Industry.

The Thursday afternoon program will be given to