The Centenary

of

Gregor Mendel

and of

Francis Galton

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MENDEL AND HIS CONTEMPORARIES

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In law the *death duty* is a tax imposed on the transfer of property at the owner's death. It is a tribute which the legatee pays to the public in return for an acknowledgment of title to his inheritance. To-day we publicly pay a death duty for the intellectual legacy which we as biologists have received from Mendel and his contemporary fellow-workers. We meet to proclaim our indebtedness to the men who found the study of heredity buried in the depths of a hazy mysticism, and left it one of the most firmly established branches of quantitative biology. There is an element of affection apart from the sense of justice in making this acknowledgment. We know that nothing that we can say here will add to or detract from the merits of these men of the latter part of the nineteenth century, but we wish to say a few words of homage as a free-will offering to the excellence of past greatness.

I was quite proud of the above paragraph when it was first written. Having listened attentively to several political orators on Memorial Sunday, I felt that it had just the proper shade of artistic solemnity expected on such occasions. In fact, it seemed as if both custom and decency demanded a series of eulogies attuned to a motive resembling the Dead March from "Saul." But I am told that this apparently decorous procedure is a mere subterfuge which deceives no one who has been taught the rudiments of interpreting the subconscious. What we really do in a case like this, I learn, is to use it as an opportunity for releasing various over-compensations from the springs of our own vanity. These supposed tributes are defense reactions. Their true purpose is to show how much better is the scholarship of the present day — that is to say, our own scholarship — than any which went before. Our motto is *De mortuis nil nisi bonum,* but our memorial wreaths are twined with poison ivy. We are not far from following the intent of the epitaph of the gentleman of the frontier, without a single redeeming quality, without a single friend, whose fellow-townsmen marked his last resting place with the truthful inscription: “In memory of John Black the citizens of Crimson Gulch are happy to erect this monument.”

One is doomed, therefore; if he escapes Scylla, he is certain to be wrecked on Charybdis. According to my informant, if one praises, his encomiums are accounted like those of him who expatiates on the superb tennis of the opponent he has just beaten; if he is critical, he lacks the good taste to conceal either his envy or his egotism. It is disturbing thus to be initiated into the secret sordidness of the human soul. I had intended to utilize this auspicious occasion to inquire into the *reasons* for Gregor Mendel’s successful masonry in laying a solid foundation for twentieth-century genetics. It appeared to be a worthy academic question which might have a modicum of importance in determining future trends in biology. I could have entered the affair stimulated by the valor of ignorance, like the Honorable William Jennings Bryan, and have said whatever seemed fitting; now I suppose I ought to be as circumspect as a speaker at a birth-control meeting with Anthony Comstock on the front seat.

Fortunately one need neither admit nor deny the contentions of these psycho-analysts. Let the actual personal motives for our actions be what they may, there is an obvious reason both for praising and for criticizing in this particular memorial celebration, which ought to be satisfactory to all concerned. Whether we belong to the aristocracy or the proletariat of science, whether our day be the nineteenth or the twentieth century, let us do one another the honor of believing that each can be counted among those who seek the plain unqualified truth. If, therefore, we do not judge those of the past as carefully as those of the present, we do both an injustice; in plain language, we are insincere ourselves, and we assume that our predecessors were such false scientists as to prefer hollow eulogies which lead nowhere to critical discussions which might aid in banishing error and fallacy.

When one speaks of co-mendelian genetic biology, he must include the sixty years previous to the beginning of the twentieth century if he is to obtain any enlightenment on the subject of Mendel’s triumph. During this period there were three types of work in progress which contributed directly to the establishment of genetics — experimental breeding, morphology and demographic mathematics. If one should undertake to enumerate the investigations which contributed their mites indirectly, he would be compelled to list every advance in knowledge made, for science seems to be like the colonial protozoan, faring best when cultivating interdependence.

The experimental breeding of the time was plant breeding. Animal breeding, of course, was much older; but as a method by which to discover new facts in pure science, it remained in the same stage of moribund quiescence from the time of the Babylonians, until rejuvenated by the quantities of interstitial tissue inserted by the zoologists of the present day. Plant breeding in England, France and Germany, on the other hand, had established several very interesting truths, such as the similarity of reciprocal crosses, the high variability of hybrids of the second generation when compared with that of the first, the dominance of characters and the reappearance of characters after being lost in the melting pot of the first hybrid generation. The names of the workers who made these discoveries are familiar. Among them are Gärtner, Godron, Lecoq, Herbert, Naudin, Vilmorin, Klotzsch, Carrière, Wichura, Hildebrand, Jordan, Haeckel, Henslow, Focke and Darwin; but with the exception of Darwin, I doubt whether any one of us could say who they were, what was their training, how they worked or what they added to the world's knowledge. Presumably they were all worthy men, who, outside of the ignominy of being botanists, had nothing to their discredit; yet if they can not be termed the unknown soldiers, at least they are the unremembered soldiers, of genetics. Why? Is the growth of science essentially so slow and so continuous that our attention is attracted only by a sudden showy change, which, like the bursting of a chrysalis, is merely the sequel to something of more importance which went before? Or, does a particular piece of work, such as that of Gregor Mendel — or rather Johann Mendel, to give him his correct name, have a value *per se* which transcends the others completely? Probably both questions should have affirmative answers. I think that all too often the unknown private deserves a considerable part of the credit usually given to the colonels and generals and chiefs of staff; but in this particular case, there is evidence of a real value to Mendel's contribution which puts it in a separate class. In this array of names are competent men, who worked hard and intelligently, who made discovery after discovery; but it would have made little difference to twentieth-century genetics if they had been tailors or bricklayers instead of plant-hybridizers. I think we need not lack in respect for every one of them if we say frankly that they did not deliver the same class of goods. Mendel was familiar with the results of the earlier researches through Gärtner's huge compendium of investigations on plant hybrids, and he had read both Nägeli's paper on hybridization and Wichura's account of inheritance in the willows which appeared in the same year as his own work. There is no evidence of his knowledge of the investigations of the French horticulturists of the period, Vilmorin, Carrière, Godron and Naudin; but had he known them thoroughly, he would have been under no necessity of modifying the statement in the preface of his paper, wherein is shown more. clearly perhaps than in any other place his grasp of the essential requirements of science. He says:

> Those who survey the work done in this department will arrive at the conviction that among all the numerous experiments made, not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which the offspring of the hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations.

Morphology, or rather the part of morphology concerned with cell development and in particular with germ-cell development, was not in the same case as experimental breeding. The cell theory had not only one great paper in the latter half of the nineteenth century — it had fifty, each of which gave real insight into the subject. In fact, by 1895, knowledge of the cell was almost as far advanced as it is to-day. It is doubtful whether even the facts which flooded from the pedigree-culture work between 1902 and 1912 were either so numerous or so valuable to general biological progress as were those discovered by cytologists between 1877 and 1887. The mere mention of names like Van Beneden, Carnoy, Fleming, Oskar Hertwig, Strasburger and Boveri, is sufficient to call to mind what master craftsman flourished in those days. No man could take *their* papers and point out that they had failed to avail themselves of the possibilities of the method of attack used. In so far as the method had possibilities, they were turned to account.

Of demographic mathematics, the third type of work useful to genetics directly, less can be said. On the purely mathematical side, the theory of probabilities, which, during the last two decades has been found to be of such great value in solving biological problems, had long been developed far beyond the immediate needs of biologists or their ability to apply it. Such application as it had throughout this period was largely as a means of grinding out various conclusions from human vital statistics; and the results were used by economists and by life insurance actuaries rather than by biologists. I doubt whether any attempt had been made to apply the method to the solution of fundamental biological problems before the efforts of Mendel and Galton, although Quételet did use it in certain special anthropological researches.

This being the state of affairs at the time, can one by its consideration draw any helpful conclusions as to the degree of success or failure attending the efforts of the various workers involved? Such an attempt, I believe, is not altogether hopeless or wholly worthless. It is the type of introspection which every investigator ought to turn to now and then for the good of his own researches.

Let us assume the present stage of genetic thought to have been reached by a single extended and inclusive investigation, and that the technical requirements of this investigation can be determined by the simple biblical rule of judging the tree by its fruits. Having found these requirements, we can apply them as a yardstick to the actual investigations of the past and present. Without wishing to be dogmatic in the matter, I find them to be four in number. This is on the assumption that there will be no disagreement from the conclusion that science advances most rapidly by the use of the inductive method. They are: (1) the development of worthy laboratory methods, (2) the control of extraneous variables, (3) the determination of quantitative relations between the phenomena studied, and (4) the translation of the results into useful terms. The first three requirements are self-explanatory. By the fourth, I mean to say that science must have adequate shorthand formulae by which extensive data can be expressed concisely, and that these formulae must in turn be easily transformed into the everyday language of perception. Mendel's own system is a good illustration. Perhaps, like Archimedes, one also needs a fulcrum on which to rest his lever. It seems to me that many a piece of investigation fails to achieve the result which might well have been expected from its general conception and execution, because it begins in the middle of a complex problem and therefore has not the proper background of knowledge to carry it through. It tries to solve the cryptogram by taking a small sample from well toward the end. It usually works out much better to begin at the beginning, or at least where the other fellow left off.

Nothing novel is presented in this particular segregation of science essentials, and probably it is not so good a division as others could devise, but I believe that by keeping even this makeshift in mind, one can see rather clearly where the various contributions under discussion belong in the general scheme of things. It also gives one the opportunity of making a fair guess as to why Mendel's paper, which was in its way a model in form, remained with uncut pages for 35 years. He himself was fond of cheering his spirits by exclaiming "Meine Zeit wird schon kommen," but unfortunately it did not come until 16 years after his death.

Let us first endeavor to visualize the trend of thought during this period. There is first the host of hybridizers. Mendel took care of them in the sentence quoted. Without a proper background of facts, they had tried to solve these genetic problems having the greatest complexity. They had gone in for generic crosses by preference, and for species crosses by compulsion. Apparently it never entered their minds to make a cross between two nearly related varieties in order to simplify the complexity of the problem. They had the simple technique necessary for the particular mode of attack used; but they made no attempt either to eliminate controllable variables, to determine precisely the relation between the facts observed, or to reduce their discoveries to a system useful for predicting the consequences of like causes.

Turn now to the work of the cytologists. Naturally, in 1865, what we now accept as the fundamental facts were practically unknown. Only 15 years before botanists had been staging a battle royal on the subject of whether Schleiden's erroneous ideas regarding fertilization were true. The literature on the female gametophyte begins with Hofmeister in 1858. Real knowledge of the male gametophyte dates from Strasburger's paper on cell-formation and cell-division in 1877. The actual cells concerned in the fertilization of the higher plants were not described clearly until 1884. And the zoologists were no more clairvoyant than the botanists. Virchow did not develop the theory of cell continuity until 1858, and his papers, as is usual with new ideas, provoked attempts at scientific sabotage for a decade after that time. Fertilization of the egg by one spermatozoon awaited the demonstration made by Oskar Hertwig in 1875. The identification of the cell nucleus as the most important vehicle of inheritance, though suggested by Haeckel in 1866, was not made until it was emphasized to the world by the independent investigations of Strasburger, Hertwig, Kölliker and Weismann in 1884; and the reduction division of the chromosomes was not shown clearly until the appearance of Boveri's work on Ascaris in 1887. The general constancy of chromosome number, their individuality in size and shape, and the details of their behavior during maturation and fertilization did not come until well within the limits of the present generation.

But one must not be blinded by this course of events. Mendel's paper shows a clear grasp of the gross facts of fertilization, and those gross facts were sufficient for his needs. Furthermore, though, the cytological details which would have made it easy for others to grasp the full significance of the paper were not available until the second decade after publication, it must be remembered that recognition of his work did not come until 15 years after these details were common knowledge. For these reasons I can not believe that it is correct to account for the peculiar neglect of Mendel's work by assuming it to be ahead of the biological *knowledge* of the time.

Let us look a little closer at the problem. Cytology has been said to be the statics, and controlled breeding the dynamics, of genetics. Perhaps there is enough truth in this analogy to show a slight difference in point of view, but even this is doubtful: they are both statical in nature, and differ most in the limitations imposed by the mode of attack. For example, if one were to take all of the facts discovered by pedigree culture work, he could infer a certain organization and mechanics of operation in the germ-cells; if, on the other hand, one were to correlate properly all the discoveries of cytology, he could draw rather accurate conclusions regarding the actual transmission of characters. Genetics could not have developed as it has without both points of view, however, for *a priori* possibilities, unless tested, have no essential value. But granting this to be the truth, even the most ardent cytologist will admit that from the broad point of view of general genetics, his calling has its defects. It has a beautiful technique; but the very fact that the laboratory methods are so refined makes it difficult to eliminate the obscuring influence of extraneous variables by the very commonplace contrivance of investigating large quantities of material under controlled conditions. Again, it is practically impossible, due to the nature of the method, to investigate material in such a way as to obtain an adequate statistical representation of the facts which will permit verifiable predictions to be made. One does not decry cytology in making this statement. Cytology deserves the highest respect. But it is necessary to point out the inherent difficulties under which the cytologist works, difficulties which make his accomplishments so much more to be acclaimed. He was in much the same predicament which one might imagine would be the plight of a group of scholarly Martians who found a stranded aeroplane out of gasoline. Using the best method under the circumstances — the cytological method — they would dissect the strange visitor carefully, and make the most minutely accurate drawings of the various parts. They would then speculate on the use of each part, and finally form a hypothesis on the value and use of the apparition as a whole. This procedure would be perfectly proper. Without it, they would probably be in a quandary to know what to do with the can of gasoline dropped overboard by the unfortunate birdman and finally found by a young Martian piscatorial expert at the bottom of a canal ten miles away. With it, the gasoline would be poured in the tank, and the hypothesis tested forthwith. Now my belief is that Mendel found the can of gasoline and by his own method of reasoning knew what to do with it. But after stealing in at night and making the apparatus run, his fellow-countrymen were not able to understand his account of the machine, because the method of dealing with it was so foreign to their own experience.

I am speaking absolutely seriously. It will not do to attribute the plight of Mendel's researches to the limited circulation of the. Brünn journal, for it was received by all the various universities of Germany and by many foreign libraries. It was due to a different cause, the inability of the biological mind to adapt itself quickly to an experience it had not had before. Mendel was not really a biologist though he investigated the heredity of both plants and animals — you will remember that he worked with bees as well as peas, though the records of his experiments with the honey-makers have never been found. Biology was one of his numerous avocations, like playing chess, organizing fire brigades, running banks and fighting government taxes. He was really a physicist, and brought to one of the great problems of biology the attitude of mind and the quantitative method of attack which had been in use for some time by physicists and by astronomers, and which was just coming to be used more widely by chemists. It was an unknown language to biology, though it fulfilled the essential requirements of scientific research better than anything which had gone before; and it came to biology at a time when those who were endeavoring to investigate inheritance by means of hybridization were not prepared for their task, and thirty years before the results of the slow-going cytological method of attack had progressed so far as to permit the formulation of a well-rounded hypothesis near enough to the truth to make it possible to outline the points to be verified and to make recognizable a plan of verification. Great as was the advance in cytological genetics during the latter half of the nineteenth century one can not imagine an appreciation of the Mendelian type of work by any of the investigators. Their minds were too carefully focussed on the individual fact. Either Darwin or Galton would have seen the truth clearly; but then Darwin and Galton were amateurs who were not trammeled by professional connection with the guild of biologists.

One finds additional reasons for accepting the point of view that it was the *method* which made Mendel's paper great, and the *novelty* of the method which made it unappreciated, if he studies carefully the generalized hypotheses on the subject of heredity during the nineteenth century. Really one does not need further demonstration if he has followed genetics from the time it passed out of the larval stage in 1900, and has seen how many of us assume we are exhibiting a fine degree of super-scientific criticism instead of mere stupidity when we adopt the agnostic attitude toward novel genetic methods and newly discovered facts. But the pernicious influence of abstract theories on the mind, the seductive way in which such theories lead away from reality, is worthy of a word on its own account.

Paucity of facts did not prevent the author of yesterday from putting forth theories of heredity by the score. One has only to examine some of the huge tomes on heredity of 30 or 40 years ago — Nägeli's "Abstammungslehre" is a good instance — to realize that lack of knowledge was even an aid to the publishing business. Nägeli was able to write whole chapters on certain subjects manifestly because he had absolutely no information on them.

Each and all, these theories were as one in using mechanical interpretations which postulated active ultra-microscopic living units endowed by their creators with various qualities. No doubt this was just and proper. Such concepts have been found useful in various branches of science, and have been retained in the current theories of heredity. I only wish to point out that many of the hypotheses, described in such fanciful detail, have been hindrances rather than helps. If each of us were asked privately to state the object of scientific hypotheses, we should probably say, "to help formulate tests by which various assumptions can be justified or refuted." But publicly, in the class-room, and in the journal, we are very likely to become enamored of a well-presented hypothesis which does not stimulate research a whit, just because we are beguiled by its plausibility. Certainly a great many of the points discussed at great length by these early geneticists do not fit any better into a scientific discussion than would Cotton Mather's disquisition on the number of angels who could deploy on the point of a pin.

Recall Darwin's provisional hypothesis of pangenesis, as he termed it, proposed in 1868. His units were the gemmules, which were being given off constantly by every cell, including the germ-cells. That was virtually all there was to it, though it was propounded as a theory of heredity. In reality it was a prop, and a very weak one, to the theory of evolution. Darwin postulated this brisk inter-cellular trade in gemmules in order to show the literal-souled biologist how acquired characters might be transmitted. On the assumption that somatic modifications are not inherited, it was unnecessary. With the latter view, the cells might just as well have been insulated from each other as thoroughly as the wires in a telephone cable. Though it be sacrilege to say it, this was not the type of production to be expected from the author of the "Origin of Species." Apparently it stimulated but one experiment, Galton's blood transfusion experiment, which we now know could have told him nothing one way or the other. It acted rather like Aaron's rod, with ink gushing out in place of water, and this effect was not for the good of science.

The most notable among the various modifications of this type of theory was that of DeVries, published in 1889. Here the corpuscles, which he called the pangens, represented potential elementary body characters rather than cell qualities, and the universe of their activity was the cell rather than the body. DeVries's theory, perhaps, was some small philosophical advance over that of Darwin, but neither was a real working hypothesis in which the possible mode of hereditary transmission was outlined in such a manner that the biological student was led to make experimental tests of the postulates involved. No doubt general evolutionary thought was somewhat clarified by their introduction into the literature of the day, but they stimulated words rather than work.

Nägeli's "Abstammungslehre," which appeared in 1884, has been credited with being the first theory of heredity endowed with qualities calculated to induce research. But was it such a theory? Nägeli proposed to distinguish two kinds of protoplasm built up of physiological units, the micellae; the one was wholly nutritive in function and required no special architecture; the other, the idioplasm, was a structure of elaborate constitution built up from micellae representing the potential characters of the organism. I can find nothing more in Nägeli's work, and it took him 822 pages to say this. Here was a man to whom Mendel had written in detail about his work during the years between 1866 and 1873, a man who had contributed notable papers to botany on subjects ranging from the form of the starch grain to hybridization, a man who discoursed at such length on chemistry and physics that one might suppose him to have had the greatest sympathy for the highest type of useful quantitative work; but he devotes absolutely no time or energy to discussing the one paper which might have shown him a way out of the wilderness in which he found himself. Was this science? I do not believe it was. It may have been only the garrulity of senility, it may have been philosophy, but it certainly was not science. There is no evidence whatever that it stimulated a single investigation or was the source of a single discovery. But Nägeli was no worse than the other theorists of his time. The three hypotheses mentioned are fair samples of some twenty or thirty which were proclaimed to the world during the last half of the nineteenth century. They have been cited only because they show, as nothing less concrete will show, where the unreal leads.

The obverse of the medal can be illustrated by Weismann's presentation of the subject.

In Weismann's theory, the idioplasm, or germplasm, was identified with the chromatin of the nucleus. The ultimate living unit, the biophore, was a kind of biological atom active in building up organic characters. They grouped themselves together into determinates which controlled the specialization of cells. The various determinants of an organism made up the ids contributed by past generations. The ids might be one or many; and where more than one might differ slightly among themselves, thus providing for variation within a species. The ids formed the chromosomes or idants by arrangement in a linear series.

These postulates seem simple enough and not unlike those of earlier theories, but the way Weismann reasoned in endowing his corpuscles with qualities was a distinct advance. It was made possible by his thorough knowledge of embryology in which he had previously made notable contributions.

Denying the inheritance of acquired characters, and doing much toward demolishing the fallacious logic put forth as proof at that time by adherents in the belief, Weismann outlined a very stimulating conception of heredity on this basis. The immortal germplasm was assumed to be set apart at a very early cell division and passed along unchanged to the next generation, except as the activities of the living units produced occasional changes in its constitution. A provision for accurate equational division of the chromosomes and their reduction in number at the maturation of the germ cells was thus demanded, predicted and afterward realized — though not precisely in the way he supposed — by discoveries in the field of cytology.

Weismann further accounted in part for evolution by a selective struggle between the determinants of the germ cells, and for individual development by a qualitative distribution of the determinants of those cells set apart to build up the bodies which were to act as hostelries for the immortal germplasm.

No matter what views one holds as to the precise amount of truth contained in Weismann's generalization, it is obvious that it is very different from the others mentioned. Many geneticists believe the modern theory to be the outgrowth of Weismann's ideas. Wilson says he brought "the cell theory and the evolution theory into organic connection." Morgan credits him with the basis of the present attempt to interpret heredity in terms of the cell, in that he suggested three of the principles used in this interpretation. Be this as it may, there is no doubt but that Weismann was the first to utilize all the facts at his command, and to utilize them very ingeniously, in building up a theory of heredity, which, whether true or not, had numerous points that could be tested by experiment. In my opinion, it is by this criterion of ultimate usefulness and not by any analysis of its content of reality, that its greatness should be measured.

This presentation of nineteenth century genetic work necessarily having been very sketchy, no apology need be made for summing up the points of the thesis involved. Mendel initiated a method whereby the elementary quantitative relationship between hereditary phenomena could be tested and retested, and expressed his results in an algebraic notation of greatest usefulness. He thus supplied to genetics an essential methodological requirement which it previously had lacked. The significance of his offering is now apparent; but the history of both genetic research and genetic theory show that biology was not ready for such a profound change at the time. The investigators were satisfied with defective methods because they were yielding important results, and were capable of continuing to yield important results up to a certain point; and those who theorized, not realizing the defects of the current methods of research, wandered about aimlessly in the universe of the unreal. Obviously, if one is to find a clear exposition of genetic thought anywhere, it should be in the generalized theories of heredity. Taking them in the order of their issue, there ought to be a history of the development of this thought. And it seems to me that they show clearly that previous to 1890, biology was unprepared for the quantitative method of physics and chemistry; yet this method was a prerequisite for continued progress. Let us put the matter in another way, for the sake of emphasis. The older methods of genetic research were inadequate, the breeding work because the workers did not know how to use their tools, and the cytological work because the workers lacked the proper tools. Nevertheless, they made progress. They built slowly but firmly an edifice that future generations may well admire, much as the laborers of ancient Egypt built the pyramids. Finally, there arrived the point when a man like Weismann could piece together a well-rounded theory of heredity based almost wholly on this cytological evidence, which was testable by experiment. But for the tests required a new method was necessary, and this method was not forthcoming until the discovery of Mendel's long-forgotten paper. From that time onward, genetics entered a new era.

Properly, this paper should come to an end at this point; but I can not stop without delaying a moment to pay a passing tribute to Francis Galton, even though I realize that Dr. Harris will do full justice to his memory. Galton, as mentioned before, was one of the few of Mendel's contemporaries who would have appreciated his work. He was a kindred soul to Mendel, a brilliant amateur, interested in everything; and but for a matter of mere chance, he probably would have reached the same goal. The matter of chance was the study of ancestors instead of descendants. It seems a minor point, but it turned out to be important. Thus the Fates play with mankind. Galton was a leader of thought in England; he was no novice in biology; his capacity in mathematics was unquestionably great; and he turned instinctively to experiment. If only this single slender thread had not obstructed his efforts, one can well imagine how far he would have gone. But perhaps it is all for the best. Statistical theory needed Galton's guiding hand. It would not be the same to-day had it not received the quickening touch of his genius. Peace be unto his name!

Morgan, T. H. 1923. The bearing of Mendelism on the Origin of Species. *The Scientific Monthly*, 16: 237-247.

The Bearing of Mendelism on the Origin of Species

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Students of genetics have often been challenged to state the bearing of their work on the old controversy about the origin of species. If the challenge has often been allowed to go unanswered, it is not because geneticists failed to have an inkling that their results might, in the end, have a significant bearing on this question, but rather because they recognized the need of first putting their house in order. The futility of attempting to arrive at any reliable conclusion concerning the origin of new types until something more was known about heredity had become only too manifest during the debates of the latter half of the last century. It required no subtlety on the part of geneticists to see that only those characters can take part in the process of evolution that are inherited. It seemed to follow that it would be better to find out what characters are inherited and how they are inherited before the controversy could be continued profitably.

Geneticists do not make any claim to have solved the problem of the "origin of species." I am afraid to "protest too much," for fear that you may conclude that we really do think so. We can (and we know that we can) furnish certain evidence — important evidence, we believe — that bears on the origin and mode of inheritance of new types. It is this evidence that I am going to consider to-day. How far these new types furnish the variations that make new species may depend on what we call "species." If, as some systematists frankly state, species are arbitrary collections of individuals assembled for the purposes of classification; or if, as other systematists admit, there are all kinds of species both in nature and in books, it would be absurd for us to pretend to be able to say how such arbitrary groups have arisen. It is possible that some of them may not have arisen at all — they may have only been brought together by taxonomists.

I am not criticizing the taxonomists, but I am letting you know that I know that we are embarked for the next quarter of an hour on a hazardous undertaking.

I am not sure, moreover, how far students of taxonomy want our help. They suspect us a little, bearing gifts. I am not sure just what they could make of our conclusions if they accepted them. The systematist may be quite right in following his own methods of arranging the animals and plants living on the globe to-day; he may be quite content to allow the geneticists to make a different arrangement. Neither is quite decided at present whether or not to let the other alone. However, there should be no quarrel between us! On the contrary, I have never failed to find that we have innumerable points of contact. I am of the opinion that we can be of mutual assistance, and I sincerely hope the systematists present will agree in this pious wish.

The *modus vivendi* that I suggested a moment ago, seems to me to have its points. Is it not possible that the kind of classification the taxonomist needs for purposes of identification may be very different from the classification. that the evolutionist needs to indicate lines of descent or of relationship? Is it not possible that the geneticist may need still another classification to indicate how many genes certain types have in common and in how many they differ? Each of us might, if he wished, erect a species definition of his own, and each would be within his rights in forming such a definition. Whether it would be desirable for the evolutionist to use the word "species," that tradition has assigned to the systematist, is a question for the evolutionist to decide; but, as I have said, it is a perilous adventure for a geneticist to attempt to interpret the historical species in terms of genes. It may also be a work of supererogation.

Hence, whenever I refer to species, in what I am about to say, it is very probable that I shall sometimes use the word in all its vague implications — much in the same sense in which Darwin used it; but when sharply defined issues are at stake I shall try to remember to use other words.

ANIMALS AND PLANTS UNDER DOMESTICATION

Darwin's largest single contribution to the origin of species grew out of his observations and experiments on "Animals and plants under domestication." Here also is the field in which modern genetics has reaped an abundant harvest. Taken broadly the results have strengthened Darwin's thesis that by artificial selection man has brought about those adaptations to his needs, or to his fancy, that our domesticated products show. Granting that some of the variety shown by cultivated plants and domesticated animals has also been obtained by outcrossing with different wild races, there still remains a good deal that appears to have arisen by the selection of new mutant characters that have appeared under domestication. It is seldom possible to tell whether a variation was obtained by outcrossing, or by mutation; but, if, as I shall try to show, the heritable differences that distinguish wild types and races also represent mutant changes in the germ-material, then it makes practically little difference whether new characters arise in nature (and are later incrossed), or under domestication (and then inbred).

The evidence that all heritable variations may have had the same kind of origin rests on the following facts and argument: We have found that the mutant types that appear in our cultures follow Mendel's laws of inheritance; practically all the character differences of domesticated races also fall under these same laws; it can scarcely be questioned, therefore, that we are dealing in both cases with mutant characters.

There are also records of mutants appearing under nature that have been found to follow Mendel's laws. There are also cases in which wild varieties, differing from each other in distinct characters, have been shown, when crossed, to come under the same laws.

This accumulated evidence speaks strongly in favor of mutants as furnishing the basis for artificial selection, regardless as to whether the mutants have appeared under cultivation or in nature.

Darwin knew about mutants, calling them sports; and, as everyone knows, he rejected sports as furnishing the kind of steps that the evolution of species seemed to call for; because, he said, such gross modifications of particular parts of the body as are seen in sports could rarely be adaptive. Only by small changes in a great many parts could arise those interrelations of parts necessary for survival.

To-day we agree with Darwin that such extreme variations as those he called sports would rarely, if ever, have contributed to the formation of new types in nature. But we also know that minute differences also arise as mutants, and that these are inherited in the same way as are the larger mutant changes. It is also now clear that these smaller mutant variations must be those small heritable variations that Darwin himself appealed to as furnishing the materials for organic evolution. In these respects we have made great advances in knowledge since Darwin wrote; and I doubt if a single geneticist familiar with the evidence at first hand will hesitate to make this substitution. We have learned to distinguish between those individual differences due to the environment (that are not inherited) and those that arise as mutations (that are inherited). Superficially there is no way of telling one from the other, since they overlap and involve the same changes in the same characters. But by pedigree work the essential difference can be made evident, as Johannsen demonstrated in 1909.

What was not entirely clear, when Darwin wrote, has been set straight. This is one of the most notable advances in the study of variation since the publication of the "Origin of Species."

MULTIPLE EFFECTS OF SINGLE CHANGES IN THE GERMINAL-MATERIAL

We have also discovered another most significant fact about those changes in the germinal material that produce mutant characters. It has been found that a single change in one gene often affects the animal or plant in more than one way; sometimes in many parts of the body. Even very different kinds of organs are often affected by the single change. Students of genetics have known for some time that the so-called unit character is a fiction — one that may have been excusable in the earlier stages of the work, but one no longer tenable or desirable. To-day we are familiar with many cases that show the multiple effects of a single change in the germ-material.

It is true that we still find it convenient to single out that effect of the gene that is sharpest, most easily observed and most convenient in the separation of Mendelian classes. We often visualize this particular effect as the single result of an alteration in the germ-material; but no practical geneticist forgets that as a rule many other effects are also produced by the same mutant change. DeVries laid emphasis on this point. He regarded each mutant change as one that affects the individual in every part — made a new elementary species out of it, he said. I think de Vries' view is much nearer to what we actually find, when mutants appear, than is the view that over-emphasizes unit-characters.

If, then, as I have just said, we pick out a superficial effect of the mutant change, as the symbol of that change, we do so because we can most easily follow its course in heredity. We ignore as a rule other subsidiary changes in the organism, such as those involving physiological processes; but the literature is full of incidental references to such subsidiary effects. Pearl's recent studies of the length of life of mutant races open up a new field of investigation in which the physiological by-effects of superficial mutant characters probably play an important rôle. It need not be argued, I suppose, that slight changes in the physiological effects of a character of a species are those that most nearly affect its chances for survival. I think it would he rational to take for granted that changes of this sort have been the ones that have played the most important rôle in evolution. Now reverse the argument! If beneficial mutant changes, involving physiological changes, also often affect superficial parts, it is the latter, being visible, that might be chosen as the mark of the species. Here we may find an answer, I think, to the old riddle, that while natural selection is supposed to produce new species by the selection of variations essential to the life of the species, our definitions of species are based almost always on trivial, superficial characters that have, so far as known, no survival value.

In other words, the systematist has followed the same course as the geneticist. He has chosen superficial differences as the distinguishing marks of his species — he has not been concerned with the characters that have in reality created the species.

If, then, physiological changes have most often been the basis of natural selection, it follows that we may get into an inextricable tangle, if, taking the systematist's definition of species, we attempt to harmonize such a definition with physiological differences between species to which the taxonomic definition has only a secondary relation. I am inclined to think that a good deal of unnecessary worry can be traced to this source.

LOSSES OF CHARACTERS AND ABSENCES IN THE GERMINAL MATERIALS

Within the ranks of geneticists themselves doubts have sometimes been expressed as to whether *any*, even the smallest, of the mutational changes that we study are of such a kind that they could produce the advances in complexity that evolution is supposed to demand. I shall not try to avoid this issue by pointing out that evolution is also sometimes backward as we say, *i.e.*, towards simplification. It may be conceded at once that many, perhaps nearly all, of the mutant types, that appear in our cultures, show not only deficiencies and losses of characters, but even that most of them could not possibly have any significance for progressive evolution. These admissions do not exhaust the subject by a long shot.

Let us look a little deeper into the situation. No one doubts that each animal and plant is adjusted in a great number of ways to the complex environment in which it lives. We can imagine hundreds of changes in any animal, but it is difficult to suggest one that would certainly be an improvement, when all the many sides of its existence are taken into account. Is it not clear, then, that almost every random change must be a disadvantageous one? This is what we actually observe when a new modification of an old character takes place. But note! Among the multifarious possible changes there *may be one* that is an improvement, in the sense that the new animal is better adapted to the old environment, or that it can better adjust itself to a slightly different one. This possibility suffices for natural selection.

In the limited range of our personal experience it is not to be expected that the mutations we find would be advantageous ones, but when we consider the vast number of individuals that make up a species, the supposed difficulty does not appear insuperable.

Bateson, who has emphasized the fact that most mutant changes are losses and deficiencies, draws the conclusion that loss in the character means loss also in the germ-material. If it were true, as he supposes, that loss of character is to be interpreted to mean that something has also dropped out of the germ-material, then I think we might begin to look elsewhere for the materials of evolution, for I can not follow Bateson in his suggestion that evolution may only mean a succession of losses. I believe the premises are wrong.[1] Again, when we look at this question of losses in character from the point of view of embryology, it is not in the least surprising that almost *any* kind of change in the germ-material would bring about defects in character. If each character is the end result of a long series of developmental (embryonic) stages, it follows that almost any alteration at the start will be expected to make less perfect the end result, for less perfect here means only something different. This I take it is what most often happens.

It also seems to me quite illogical to infer that because a change in the germ-material may bring about a defect in the developmental process, this change in the character is to be interpreted as a loss from the germ-material. Such a conclusion seems not only unnecessary, but, what is more important, it is in flat contradiction with the only critical evidence that we have bearing on this question. I mean the evidence from the order of appearance of the multiple allelomorphs of Drosophila.

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1 In his Australian address in 1914 Bateson’s purpose was to point out to what conclusion one is led on the assumption that mutations are losses and if mutants are assumed to furnish the materials for evolution. In his Toronto address in 1921, on the other hand, Bateson appears to argue that the distinctive differences between wild species are something added, and therefore not the kind of variation about which genetics concerns itself.

The argument advanced here in the text accepts neither alternative, but rests on the interpretation that a mutation need not represent a loss of germinal material, and that the differences between species are probably mutant differences.

Much also has been said concerning dominance and recessiveness of mutant characters in relation to the characters of the wild species. Bateson has emphasized the fact that most mutants behave as recessives to wild type characters. Hence he concludes that these mutants do not seem to be the stuff from which wild species are made. Now, in the first place, while the statement that nearly all mutants are recessives may hold in certain cases such as Drosophila, yet there are other groups in which the number of dominant mutant characters is much in evidence. But the distinction itself between dominant and recessive is by no means so general as implied. Mendel described only nine pairs of characters, choosing those in which dominance is complete. To-day, we look upon these as rather extreme cases, not as the typical ones. We meet with many cases in which dominance is imperfect. The hybrid is intermediate between the two parental types, especially when all the different modifications of the pair of genes in question are taken into account. The same gene may, in fact, be dominant in one respect and recessive in another. When the hybrid is intermediate, it is often purely conventional which alternative is chosen as the dominant. The real point at issue — Mendel's great discovery — is that genes separate cleanly in the germ-cells, even when the hybrid is intermediate. It befogs our problem, I think, to insist that dominance means complete dominance. With this sharp distinction done away with, the difficulty loses much of its apparent point.

INFERTILITY BETWEEN SPECIES AND STERILITY OF THE SPECIES-HYBRID

One of the oldest questions concerning, the origin of species by the summation of individual differences is this — how has the infertility, commonly observed when species are crossed, arisen? No incipient infertility, it is said, can be observed when different breeds of domesticated animals are crossed. Darwin had to face this question, and met it in the only possible way that it could be met at that time. He pointed out that there is in reality no such sharp distinction as implied. He showed in a large number of cases that well-recognized species do cross, and that sometimes they even produce fertile offspring.

Since Darwin's time a great deal of work has been done by embryologists that bears on this relation. Every embryologist is familiar with the fact that sea urchins belonging to different genera and families can be cross fertilized. The early stages of development of the hybrids are often normal. It is only when the conflicting processes that are induced by the inherited characters of the egg and sperm begin to crop up that difficulties set in. When we take into account the delicately balanced processes that each stage in embryonic development involves, it is not in the least surprising to find an incompatible situation when conflicting interests are brought together.

Then again, in the higher plants mechanical and physical differences may often account for the failure of the foreign pollen tube to reach the egg. Similarly, in matings between two species of animals there may be incompatible structures or responses. When such matters as these are given sufficient weight it is not going too far to claim that we are not dealing here with a single fundamental difference, but rather with several different kinds of processes that give like results.

It is true that new mutant types are fertile (if fertile at all) with the type from which they arise, because the single difference that distinguishes one from the other is a compatible difference. If it were not, the new type would be lethal. When, however, two types have been separated for a sufficiently long time, differences may be supposed to arise in one, or in both, that are incompatible in fertilization or in development. This seems to me to cover the case from a theoretical point of view.

Even the infertility often observed between the pollen and the ovules of the same plant is now in a fair way of being explained. The recent work of Correns, of East and of Compton has shown that such kinds of infertility depend on the presence of one, or at most a few, genetic differences. In such cases the failure to fertilize appears to rest on differences in the somatic tissue and not on incompatibility of sperm and egg or on difficulties in embryonic development.

That infertility may arise as a consequence of genetic differences has been shown by the recent work of Jones on corn and tomatoes. When pollen from one race was placed in competition with pollen of other races that differed only in minor features it was found that the plant's own pollen was the more efficient, *i.e.*, it fertilized proportionately more ovules. The result may fairly be interpreted as a case of *incipient* infertility in outcrosses. We do not know how frequently such a relation exists, because the problem has been very little studied with critical standards. The essential conditions for such work are seldom realized. On the whole, then, is it not a little remarkable to find in the one case where the problem has been adequately examined that the outcome has been positive?

Bateson has recently laid much emphasis on the *sterility of the hybrids* themselves in species-crosses as compared with the absence of such sterility when mutant races are crossed. In the latter case not only is there no incipient sterility in the F_1 offspring, but on the contrary the F_1 heterozygotes may, and often do, produce more offspring than do individuals of either parent race.

Bateson has laid a great deal of emphasis on the importance of this question for modern genetics. His studied wording of the requirements that would be necessary to demonstrate that interracial sterility had arisen in connection with mutation is worth careful consideration: "The production of an indubitably sterile hybrid from completely fertile parents, which have arisen under critical observation from a common origin" — this "is the event for which we wait."

Bateson has made the conditions of demonstration extremely difficult. He postulates that "the event for which we wait" is one that must suddenly occur — as a mutation perhaps? If so, and if as seems to be probable in the case of other mutations, the expected change should occur in only one gene, it would by definition make sterile the animal that received this gene, and hence defeat any effort to prove its fertility. There are possible ways of escaping this dilemma, but these would detract from the generality of such origin of sterility.

Suppose, in order to avoid the contradiction in terms just referred to, we ignore the probability that mutations take place in one gene at a time, and suppose that a single individual of the new type called for has appeared as a duplex mutant. The chances are very great that is would be lost before its value was appreciated for the simple reason that it would have to be crossed to the original from which it arose in order to get any offspring at all. It is with this type that it is by hypothesis expected to give sterile offspring. Only when several individuals of the new imaginary type arose at once, or as a bud sport, could a race be produced with which to properly test the question of sterility of mutant hybrids according to definition. These and other considerations raise the question as to whether the sterility of species hybrids may be of such a nature that we are justified in insisting that they must arise under the conditions that Bateson postulates as essential. There is at any rate another side to the question which may throw some light on the situation from an entirely different angle. It is now well known that in those stages in the development of the germ-cells, that are concerned with the conjugation of the chromosomes, irregularities occur in the distribution of the chromosomes in species hybrids. As a consequence many or even all of the germ-cells are abnormal. Hence arises the sterility observed in such hybrids. In many cases these irregularities seem to be connected with differences in the parental numbers of chromosomes. Such a situation would not be expected to arise when mutation in a single gene has made one parent different from the other, but might be expected, if, due to doubling of the chromosomes of one of the parental gametes, there is produced a triploid individual. In fact, a disturbance, similar to that in species hybrids, has been described in some at least of the mutational triploids that have been examined. It would, however, be a mistake, I think, to assume that the sterility of all species hybrids is due to differences in the parental chromosome numbers, although this may be the expectation when the numbers are different. There are other cases where the parental chromosomes are the same in number and the species hybrid is sterile; hence, there may be still other kinds of differences that make conjugation of the chromosomes difficult or impossible. One of the events for which I wait is the demonstration of such differences that interfere with the conjugation of the chromosomes and tend in consequence to produce sterility.

RECURRENT AND PARALLEL MUTANTS

Finally, the demonstration that the same mutant types recur over and over again has opened up new points of view with interesting consequences. It has long been known, in a general way, that the same kind of mutants reappear *in the same species.* We are now beginning to get evidence from pedigree cultures that the same types may occur *in different species.* At present there are only two ways in which we can be sure that the latter are due to the same kind of change in each species. One way to prove this is by crossing the two mutants. If both mutant characteristics are recessive, and give the recessive when crossed, the proof is established that they are identical mutants. Such a case has arisen between the two species of Drosophila simulans and melanogaster. Sturtevant has shown that there are thirteen mutants that are the same in both species.

The other way of showing that two mutants arising in different species are identical (isomorphs) is to find their linkage relations with respect to other mutants that also appear to be identical in the two species. This involves the possession of several such types in both species, as well as a fairly complete knowledge of linkage groups in both. It may take several years before enough material can be brought together for a safe conclusion, but the outlook is promising.

If, then, it can be established beyond dispute that similarity or even identity of the same character in different species is not always to be interpreted to mean that both have arisen from a common ancestor, the whole argument from comparative anatomy built upon the descent theory seems to tumble in ruins. This, however, is only a first impression; for, even if it be true that some of the resemblances between species may be due to identical mutational changes in the same gene, there remains the vast array of other characters that the two species still retain in common. These furnish the hint that the evolutionist needs to make probable his theory.

Should it turn out to be true that a large number of similarities in species are due to similar mutations in the same gene, then, in future, the student of genetics will be more interested in detecting these identities than in taking account of the genes that have not yet produced new mutants. The evolutionist will be concerned with the genes that still remain unchanged because these will indicate a common ancestry. But, I think, he will be at his wit's ends to exclude from his lists those similarities that are due to identical mutational changes. Lest you infer that I am letting this idea run away with me, I should like to add that we are also only too familiar with cases where mutations, in quite different genes, produce effects that are so much alike that it takes a microscope to tell them apart — and even this may not suffice. Sometimes we even have to appeal to statistics to help us out.

Nevertheless, the discovery that the same mutation happens over and over again, not only within the same species but in different species, is, I think, one of the most interesting discoveries in recent genetic work. It means that certain kinds of changes in the germ material are more likely to occur than are others. If we adopt the Galton metaphor of the equilibrium polygon, these changes might be interpreted to be the more stable conditions of the genes. Or, if we prefer to think of the change in the gene as a chemical event we can form a somewhat different picture to ourselves as to what happens. Whatsoever way we prefer to symbolize the recurrence of the same event in the same gene the significant feature remains the appearance of new variations in the hereditary material is something less a random process than we had hitherto supposed.

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GALTON AND MENDEL: THEIR CONTRIBUTION TO GENETICS AND THEIR INFLUENCE ON BIOLOGY

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Francis Galton and Gregor Mendel have much more in common than the mere incident of the identity of the years of their birth. Both men worked in advance of the science of their own generation. Both have influenced in a profound and far-reaching manner the science of subsequent generations.

The fact that they have these common characteristics must not lead us too hastily to the conclusion that there is a detailed parallelism in their lives. Neither can the linking of the two names on the same anniversary program be accepted as evidence that they are equal in intrinsic greatness or in their influence on science. It merely invites us to take stock of the work that the two men did and the movements that they set under way, with a view to deciding — if as individuals we choose to do so — which has contributed the most to the century which has passed and which has most to offer in inspiration and guidance for the future.

To this task we must turn in an effort to do the fullest justice to both men, but with that scientific candor which should characterize our attack on any problem.

II

Here lies our greatest difficulty. Scientific men are after all very human creatures. They fish in the same pools, worship at the same shrines, and sometimes have that almost pardonable human weakness of projecting haloes about a selected few of the human figures in the development of their science which are sufficiently distant in time and obscure in actual personality. In science we have no formally canonized saints. Nevertheless, we must not forget that we are to-day comparing two quite different entities — we are contrasting Sir Francis with Saint Gregor.

Here we reach our first point of contrast between Mendel and Galton. Mendel must be viewed through the halo which unconsciously but none the less definitely has been projected about him since the simultaneous rediscovery of the principles announced in his one noteworthy contribution raised him from almost total obscurity to fame. Galton's life is an open record.[1]

Mendel's life has been so often and so minutely portrayed in all ascertainable details that it will be impossible to add anything to what is already familiar. Galton's life was so rich and varied that it will he impossible to do more in the few minutes granted to me than to give a few illustrations of his achievements.[2] I shall attempt merely to balance the two personalities against each other, leaving the decision as to the relative importance of their work and the relative significance of their influence on science to the jury here assembled.

III

A perusal of the mere facts of the lives of Galton and Mendel at once raises, but unfortunately fails satisfactorily to answer one of the questions in which Galton had a sustained interest — that of the relative importance of nature and nurture in determining the characteristics of the individual. Galton came of stock of long proved intellectual power. Mendel's more distant ancestry is hidden in obscurity, and there is no evidence of great intellectual ability in the parental generation. Galton's family could and did provide for him as a boy the best that the times afforded in intellectual discipline and inspiration. The beginnings of an education were for Mendel a rare opportunity and bought at a sacrifice to his family. Galton saw the world broadly, through his own eyes and through those of his friends

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1 So detailed is the available information that a well-known psychologist has attempted to determine "the intelligence quotient of Francis Galton in childhood." See L. M. Terman, Amer. Jour. Psychol., 28, 209-215, 1917.

2 The present paper is in no sense an attempt at an abridged biography of Galton. I hope that it may stimulate the reader to read Galton's charming "Memories of My Life," which will be as fascinating to the general reader as to the professional biologist, and Karl Pearson's masterly biography, "Life, Letters and Labors of Francis Galton," which must remain for all time not merely the source of authoritative information concerning Francis Galton, but one of the most notable biographies of this century. It is much to be hoped that the near future will see the completion of this comprehensive work, long delayed by war activities.

— eminent in exploration, in science and in public life. Mendel's outlook was always limited by the walls of a narrow geographical cloister.

Yet both men have made great contributions to scientific advancement.

If for a moment I may be permitted to show partiality, and to venture at interpretation as well as presentation of facts, I must confess that it seems to me that as an individual Mendel deserves the greater credit for his achievement. Nurture fed all that was best in Galton's rich natural inheritance. Intellectual nurture was not lavished on Mendel. There may have been at one time real danger that Galton's abilities would be sterilized by luxury. There was grave danger that Mendel's abilities would never be of significance in scientific progress because of lack of opportunity.

Fortunately neither of these misfortunes was realized. In 1847 Mendel was ordained a priest, and in 1849 he was sent at the expense of his cloister to the University of Vienna, where he remained until 1853. It was in the midst of this period, in 1849, that Galton suddenly ended "the fallow years" of his life, ceased sowing his wild oats, and turned again to the scientific studies which had fascinated him before his interests had been submerged in a life which for a time had been devoted too largely to reckless pleasure.

IV

We should not proceed further with our comparison without noting that neither of the men whose birth is to-day celebrated by the American Society of Naturalists was an avowed naturalist in the more classical sense of the term nor a professional biologist in its modern interpretation.

I have searched in vain through Galton's accounts of his travels for evidence of a compelling interest in the peculiarities of the plants and animals of the extensive region which he opened up to geographical knowledge by his early explorations. He seems never to have described a species, or even to have collected them. His name is represented in the literature of taxonomy only by the South African genus Galtonia, of the French botanist Decaisne. It is perhaps significant that as an explorer Galton's natural history observation dealt not with the fascinating superficial forms of the organisms which he encountered, but with animal and human behavior.

Mendel may have been more under the influence of the biology of his own time. He wrote notes on *Scoplia* and *Bruchus* as a student. He was apparently influenced to some extent by the work of other experimental breeders. His materials were at least varied. While his chief work was with plants he devoted much energy to an attempted study of inheritance in bees.

In so far as they considered living organisms the attitude of both Galton and Mendel was more like that of the modern biologist than that of the earlier naturalist.

It is not difficult to establish this, to the complete satisfaction of geneticists, for the Abbot Mendel's greatest contribution, that on inheritance in peas, still stands as a model for much of the modern work in genetics.

Because of the greater number and the wider scope of his publications it is not so easy to pass upon the work of Galton. I fear that many of the members of this audience are unaware of the wealth of Galton's contributions. It will facilitate our subsequent discussion to detail a few of his activities. For the moment I shall limit attention to those which have an immediate bearing on modern biology. His studies of finger prints laid the scientific foundation for a widely applied means of penal and military identification. His early attempts to influence the character of the offspring by the transfusion of blood were essentially modern in their experimental viewpoint. Anthropometric laboratories owe their origin to his interest in human faculties and still profit by his early-devised methods. His studies of the inheritance of physical and mental characters, given to the world over a half a century ago, still furnish, when coupled with an attempt at Mendelian analysis, the model for much of what passes for research in eugenics. Finally, his contributions to the application of mathematical methods in the biological field have had so great an influence that they must be reserved for separate discussion in a later section.

V

The suggestion will inevitably be offered that the work of Galton and Mendel was of the nature of modern biology rather than of the older natural history of their day because of the fact that their pioneer work determined to an appreciable degree the lines along which modern biology has evolved.

Herein lies one of the most interesting points of comparison between Mendel and Galton, and one concerning which there will probably be little differences of opinion among the majority of this audience.

To those who view the vast output of genetic investigation — evident alike in our journals and in our scientific programs — there may seem no reasonable doubt that Mendel has had a more profound and far-reaching influence on biology than Galton.

I have no desire whatsoever to quarrel with the far superior numbers who hold this opinion. I would, however, like to have the facts candidly and judiciously examined.

No one can deny that Mendel's influence on biology — assuming for the sake of argument that the development of modern genetics is to be attributed largely to the influence of Mendel — is conspicuous because of the fact that it has resulted in a narrow and highly unified field of work. Galton's influence was much more varied.

Let us for the moment disregard the broader aspects of biology and of science and limit our attention to the field of genetics, as it has been influenced by the work of Mendel.

Has Mendel's influence transcended or even equalled that of Galton?

Mendel had a relatively small and certainly only an ephemeral personal influence upon the biology or biologists of his time. His published work was, practically speaking, without influence on biology for three decades. Notwithstanding this fact a number of biologists were at the time of the "Rediscovery" more or less actively engaged in experimental breeding. Three have been recognized as co-rediscoverers, and others have been known to modestly lay claim to having been near the great honor. This widespread interest and activity in the experimental attack on the problems of what we to-day call genetics can not have been a matter of accident.

I venture to suggest that there were three groups of influences which determined these activities; the lingering interest in the studies of the earlier experimental breeders; the rapidly increasing economic importance of plant and animal breeding, and the personal influence of Francis Galton and of his writings.

Let us leave for the historian the decision as to which of these was the most important factor. It is sufficient for our purpose to recall that while Mendel's paper lay unheeded Galton's pen was influencing public opinion and scientific thought. His volumes did not stand with uncut pages. They were read and annotated. "Hereditary Genius," while foreshadowed by essays[3] appearing in the same year that Mendel's paper was read, was first published in 1869. An American edition was issued in 1870, and again in 1891. A revised English edition was prepared in 1892.[4]

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3 Galton, F. "Hereditary talent and character," *Macmillan's Mag.*, 12, 157-166, 318-327, 1865.

4 An important prefatory chapter in this edition gives Galton's impressions of the activities of the twenty-three years which had elapsed since the appearance of the original edition.

While "English Men of Science" might be assumed to be primarily of national rather than of international interest, the English edition of 1874 was followed by an American reprint of 1875. His more technical volumes were issued in only one edition, but were widely read. They appealed to the more intelligent general reader, and they influenced the thought of the specialist. The volumes of Bateson and de Vries issued prior to the "Rediscovery" bear witness to their influence. Whitman's personal copies of "Natural Inheritance" bear evidence of intensive study. A perusal of the "Foundations of Zoology," penned in part over a quarter of a century ago, shows clearly how great was the influence of Galton on the thoughts of such a leader as W. K. Brooks.[5]

Nor was Galton's influence limited to that of his own writings. Weldon's earlier papers had appeared, and biology was beginning to feel the influence of Karl Pearson's pen. These were, to be sure, largely independent, but they showed, and their authors gladly admitted, Francis Galton's friendly influence.

Whether Galton and Pearson were wrong in regard to theories of heredity, or in their method of attack upon the problem of inheritance, does not concern us here. The thing which is of real importance for our present consideration is that fact that in 1901 the scientific world was ready to replace speculation on inheritance by inductive research. Some force or forces led to the profound changes in biological thought between 1866 and 1901. Certainly these changes, which may have been greater than those which have taken place since Mendel's work received recognition, were not due to Mendel. I venture to express the conviction that among these forces one of the most powerful was the direct and indirect influence of Francis Galton.

It was no fault of Mendel that the circumstances of the "Rediscovery" and subsequent events have tended to obscure the influence of Galton. The practically simultaneous announcements of Correns, Tschermak and de Vries, coupled with the discovery that Mendel had preceded them by three decades, made a spectacular setting for the new field of experimentation — a staging which was further illuminated by Bateson's controversial writings.[6]

Thus the circumstances of the "Rediscovery" were such as to place Mendel at once in the most conspicuous place on the biological stage.

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5 While Brooks did not always agree with Galton, he wrote: "My own debt to Galton is great, and it is acknowledged with gratitude."

6 Those who know the history of biology in the quarter of a century now coming toward an end must realize that the simultaneous rediscovery of Mendel's principles by three different investigators lead to an emphasis upon the priority of Mendel's work which would not have been laid if only one more recent worker had observed the agreement between the frequencies of individuals of different classes in the segregated generation and those given by permutation formulae.

From 1869 when "Hereditary Genius" appeared until 1889 when "Natural Inheritance" was given to the world and to 1901, which marked the founding of a special journal for the statistical investigation of biological problems, Francis Galton had prepared the professional and the lay mind for a dominant interest in heredity. In 1901 the seed of the "Rediscovery" fell in fertile and well-tilled soil, and Mendel reaped where Galton and his coworkers had cleared and tilled.

VI

We have already considered in a preliminary way the influence of Galton and Mendel on genetics. Mendel's direct influence has extended little beyond this one phase of biology. Galton's work and influence in biology and in science were much broader. Few biologists realize their scope, or their importance.

VII

First of all, Galton early won recognition as an explorer. While Mendel was completing his studies at Vienna, Galton was traversing the land of the Namaquas, the Damaras and the Ovampo. His trail led him over a thousand miles into tropical Southwest Africa. The regions which he traversed were mapped on the same plate which gave to the world the geographical results of some of Livingston's explorations.

It is our loss that we can not stay to review some of the fascinating chapters of his "Tropical South Africa,"[7] a volume in which the hardships and adventures of the twenty months of exploration are subordinated to serious observations on the peoples and their customs.

Impaired health could not prevent Francis Galton from contributing to the advancement of geographical science, though it did lead him to decline the opportunities for further African exploration. His editorship on "Vacation Tourists" was of but short duration, but the contents of the three volumes justified the editor's suggestion that "scientific tours offer an endless variety of results." His "Art of Travel,"[8] while in a sense a compilation, in part from the literature and in part from the personal experiences of the great explorers of his time (with whom he was in intimate association), is truly remarkable not

7 Galton, F.: "The Narrative of an Explorer in Tropical South Africa," London, Murray, 1853. The first edition was quickly exhausted, but a reprint, with a few changes, was issued in the *Minerva Library of Famous Books* in 1889. A valuable appendix, prepared by Mr. Galton, gives additional information of interest obtained during the thirty-six years which had elapsed since the preparation of the original volume.

8 Galton, F.: "The Art of Travel; or Shifts and Contrivances Available in Wild Countries," London, Murray, 1855. Various subsequent editions.

merely in clearness, conciseness and comprehensiveness, but in conception.

In evaluating the significance of his conception we must not forget that the volume was prepared at a time when the Royal Geographical Society was but twenty-five years old, when only the margins of great continental areas were even roughly mapped, and when vast wildernesses, including much of our own fertile domain, were open for colonization. Writing at this time — which was long before the acceptance of the idea that technical training might constitute a part of education — Galton wrote in his preface to the second edition:

> I am convinced that the Art of Travel, or of campaigning, admits of being taught. . . . It therefore seems to me, though I may perhaps be considered an enthusiast by many, that every intelligent youth who seeks a commission in the army, or to become an emigrant, or a missionary, should find his time and energy well spent in learning to use the axe, saw and chisel, the soil needle, the cobbler's awl, the blacksmith's hammer and the tinsmith's soldering iron together with the greater part of the bush manufactures and makeshifts of which this volume treats.

That the volume fulfilled the necessary requisite of usefulness is perhaps evidenced by the several printings which have been issued.

VIII

Time will not permit a detailed discussion of Francis Galton's work in the physical sciences. His studies can not be judged by the standards of physics and chemistry, for they have had only an insignificant influence upon the development of these sciences. Neither can his contributions be dismissed as the pastimes of an ingenious amateur. Practically without exception they indicate inventive efforts towards the practical application of physical principles in other sciences.[9]

Among such studies we may read by title only his work on a hand heliostat for signaling on sea or land, his principle for the protection of riflemen, stereoscopic maps, spectacles for divers, the conversion of wind charts into passage charts for vessels of known sailing capacities, his work on a drill pantograph, instruments for determining the upper

9 His earliest paper, printed after his departure for his early African explorations, in 1849, was on the possibilities of a printing telegraph instrument. The apparatus designed seems never to have been carried beyond the preliminary stages. The point of greatest interest lies in the fact that seventy years ago Galton foresaw clearly the possibilities of house-to-house communication which might result from a system of centrals if the telegraph instrument could be adapted to the use of individuals instead of limited to highly trained operators.

limit of audible sound, composite portraits, photographic measurement of animals, and analytical photography.

Galton's work in the physical sciences was not characterized merely by inventive skill. He was keenly alive to the necessity for the standardization of instruments at a time when little attention was given to this essential outside the physical laboratory, and he gave personal attention to the rating of watches, and the standardization of sextants and clinical thermometers, as well as to administrative work during his long connection with Kew Observatory.

IX

The widespread interest in the weather and the chaotic state of meteorological work at the time of Galton's return from his African explorations were almost inevitably a stimulus to his interest. He saw at once the importance of synchronizing and standardizing observations made at stations as systematically distributed as possible over wide areas. He foresaw instinctively the necessity for a better organization of the data then available if progress was to., be made in meteorological investigation.

It will be practically impossible for biologists, accustomed to turning to a wealth of meteorological observations tabulated and, mapped in detail for their use in studies of geographical distribution, to realize the conditions which prevailed at this time. Partly for its intrinsic interest and partly for its illustration of Francis Galton's firm grasp of scientific method and the importance of scientific organization and cooperation, I beg permission to quote the following from the introduction to his "Meteorographica"[10] of 1863:

> A scientific study of the weather on a worthy scale seems to me an impossibility at the present time from want of accessible data. We need meteorographic representations of large areas, as facts to repose upon, as urgently as experimental data are required by students of physical philosophy.
>
> Meteorologists are strangely behindhand in the practise of combining the materials they already possess. There are more than 300 skilled observers, using excellent instruments, scattered over Britain and the continent, who transmit observations taken twice daily to meteorological societies or government institutes. Besides these, are the same number of lighthouse keepers.... Lastly, many observers publish independently. Yet throughout this mass of labor that practise of general combination is absent, which is required to

10 Galton, F.: "Meteorographica, or Methods of mapping the weather," illustrated by, upwards of 600 printed and lithographed diagrams referring to the weather of a large part of Europe. London and Cambridge, 1863.

> utilize it as it deserves. No means exists of obtaining access to any considerable portion of these observations, without great cost, delay and uncertainty, much less can they be obtained in a "reduced" and never in a meteorographic form. The labor of a meteorologist who studies the changes of the weather is enormous before he can even get his materials into hand and arrive at the starting point of his investigations. In the ordinary course he has to apply, with doubtful chance of success, to upwards of ten meteorological institutes in Britain and Europe, for the favor of access to the original documents received by them, and to fully thirty individuals besides. He has next to procure copies, then to reduce the barometer and thermometer readings to a common measure, and, finally, to project them on a map.
>
> I feel that all this dry, laborious and costly work, which has to be undergone independently by every real student before he can venture a step into the scientific part of his work, is precisely that which should be undertaken by institutes established for the advance of meteorology.

After discussing some of the essential features of meteorological maps he says:

> A sustained series of publications of this kind, extending over two or three years, would give an extraordinary impetus to the scientific study of meteorology. They would supply the necessary materials in a manageable form, for arriving at a general knowledge of the distribution of the various elements of the weather; they would afford means of testing the extant theory of "forecasts" with a rigor impossible at the present time, and they would necessarily improve it.

Galton foresaw the desirability and the possibility of international cooperation, for he continued:

> If extensive tables of reduced observations were issued in England we might look for the cooperation of meteorological institutes on the continent (who already publish voluminously) in following our example.

After discussing some of the practical problems of international cooperation, he concludes:

> Entertaining the views which I have expressed on the necessity of meteorological charts and maps, and feeling confident that no representation of what *might* be done would influence meteorologists to execute what I have described, as strongly as a practical proof that it could be done. I determined to make a trial by myself, and to chart the entire area of Europe, as far as meteorological stations extend, during one entire month . . .

In evaluating the conception we must not forget the time at which it was written: It was two years before the two essays which furnished the first published intimation of "Hereditary Genius" and before Mendel's paper was read. It was at a time when for our own meteorological records we were depending upon the journals of our exploring expeditions and surveys, upon the observations of our medical officers at the army posts, and upon such systematic records as the Smithsonian Institution could assemble. Thus Galton's personally printed weather maps preceded by over twenty years our first tridaily meteorological maps.[11]

But we must hasten on; it is not our purpose to detail before a biological audience his various activities in the development of modern meteorology, during the more than thirty-four years of his activities at Kew Observatory and in the Meteorological Office.

In writing to Mr. Galton upon his resignation from the Meteorological Office Sir Richard Strachey said:

> It is no exaggeration to say that almost every room in the office and all its records give unmistakable evidence of the active share you have always taken in the direction of the operations of the office. The council feel that the same high order of intelligence and inventive faculty has characterized your work in meteorology that has been so conspicuous in many other directions, and has long become known and appreciated in all centers of intellectual activity.

I am not pretending that Francis Galton was great as a meteorologist. His work came too late in the development of the science to appear alongside that of Galileo where it might be expected in the indices of modern text-books. His personal work came too early to be connected with much of the modern development which has resulted from the widespread establishment of stations which he foresaw as an essential to the practical use of meteorological observations in the protection of shipping. It is not unreasonable to suppose that Galton's work will have greater influence upon the future development of meteorology than it has in the past, for the methods of correlation, regression and partial correlation are now being introduced into the treatment of meteorological data.

Looking back on these phases of Mr. Galton's public service, we as naturalists can not but regret that it absorbed energy which might have been devoted to studies of inheritance, and to the problems of eugenics.

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11 U. S. War Department, Office of the Chief Signal Officer: *Tridaily Meteorological Record,* issued from the Office of the Chief Signal Officer. The charts begin with January, 1878, but were not published until 1884.

But let us not forget that the scientific man is a citizen as well as an investigator. Mr. Galton's gift of time and thought to administrative duties curtailed his list of books and papers.

Have they curtailed his influence upon the progress of science?

X

I have touched as lightly as possible on those achievements of Galton which had no counterpart in Mendel's work, in part because I have wished to avoid any possible semblance of partiality in the treatment of the two characters and in part because I have desired to reserve the time for a discussion of the broader aspects of Galton's biological work.

In Galton's narrative of his African explorations there is, as I have said, little to indicate a keen interest in the flora or fauna, other than the big game. There are, however, unmistakable evidences of interest in man. To Galton the loss of valuable equipment was not merely a difficulty to be overcome. It was an opportunity to study the behavior of primitive peoples, by pitting one tribe against another in the recovery of his lost property.

In his later life this interest made itself felt in four interrelated fields of work — in anthropology, in psychology, in heredity and in eugenics.

Galton's studies in these four fields are so closely interrelated that in noting his major contributions I shall follow in the main a chronological sequence.

An illustration of the impossibility of separating them is afforded by "Hereditary Genius," his first great biological work, which appeared sixteen years after his "Tropical South Africa," and during the period of his most active interest in meteorology.

"Hereditary Genius," as Mr. Galton, tells us, grew out of a purely ethnological inquiry into the peculiarities of diverse races. In 1874 "Hereditary Genius" was supplemented by a volume on "English Men of Science; their Nature and Nurture." In 1883 "Enquiries into Human Faculty" assembled under one cover the observations, experiments and statistical studies of color blindness, capacity for distinguishing shrill sounds, criminality and insanity, gregariousness and slavish instincts, number forms, the sensitiveness of blind and seeing and of savage and civilized individuals and many other interesting topics.

It was during this period that his interest in anthropological measurements and in finger print identification developed. In 1882 he published a plea beginning "When shall we have anthropometric laboratories where a man may from time to time get himself and his children weighed, measured and rightly photographed, and have each of their bodily faculties tested by the best methods known to modern science?" As a result of his interest, an anthropometric laboratory was established. He recognized the possibilities of obtaining materials of value for scientific investigation from measurements carried out in the public schools, and utilized such materials in his own studies.

Coincident with and supplementary to physical measurements were his studies of finger prints.

Galton foresaw the difficulties of the use of the Bertillon system because of the fact that physical measures are correlated. His interest in finger prints as a means of personal identification first became generally known through a lecture delivered before the Royal Institution in 1888. In 1891 he published an extensive memoir in the *Philosophical Transactions.* His books on the subject are "Finger Prints" (1892), "Decipherment of Blurred Finger Prints" (1893) and "Finger Print Directories" (1895).

The consequence for science of these studies is not to be judged by the volume of the data, by the pages published or by the conclusions drawn. Neither will I point to the fact that in our recent world conflagration the possibility of the identification of millions of men depended upon methods for which we are primarily indebted to Galton.

The true importance of his work inheres in more subtle influences. First, these studies contributed, directly and indirectly, to the development of Galton's own grasp of the larger problems which I shall discuss in a moment. Second, they had an immediate influence upon the scientific thought of his own time.

All students of Mendel's life have emphasized the fact that his influence upon his contemporaries was but insignificant.

The case is quite different with Francis Galton. Throughout his life be was active in the affairs of the British Association, the Royal Geographical Society and the Anthropological Institute. During his later years when his own pen was less active his personality was an inspiration to the scientific men with whom he came in contact, and many of them owed their success in no small degree to his kindly interest. They, in their turn, extended his influence. In America, for example, the early development of both experimental psychology and of statistical methods in anthropology is in no small degree due to J. McKeen Cattell's early association with Francis Galton.

It is hardly too much to say that the personal influence of Galton was one of the chief factors in the development of anthropometry from anthropology. His influence upon the development of experimental psychology was probably equally great.

XI

This brings us to what is the next to the most important if not the most important phase of Galton's work and influence.

The facts which any one individual accumulates can generally be discarded without serious loss within a few years after the good which he has done is interred with his bones. While Galton's contribution of facts constitutes a much larger fraction of the literature of biology than does that of Mendel, it has long since been replaced by better or more extensive data and his name rarely appears in the "Literature Cited" of our current journals. Galton's really great contribution was that of method.

Here again we arrive at a certain parallelism between Galton and Mendel. In their influence upon the methodology of science Galton and Mendel had two things in common.

First, they both recognized the value of a direct appeal to experimental or observational facts as contrasted to speculation and authority. They differed in that Mendel appealed to experimentally determined facts, whereas Galton laid greater emphasis upon the statistical analysis of observations and measurements.[12]

Second, both showed biologists the value of replacing the irregularities of observational frequencies by a smooth mathematical formula.[13] A permutation formula-for example, that leading to the 9:3:3:1 ratio — is a mathematical expression fitted to the empirical data just as truly as is the normal curve.[14]

XII

Galton's work in the application of mathematical methods to biological problems extended much farther than the mere description of frequency distributions by mathematical formulae. He grasped the important conception that in biology we are chiefly concerned with the

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12 The difference was in no way due to a lack of sympathy on the part of Galton with experimental methods, but rather to his keen interest in man — an organism which is not available for experimentation in the same way as are peas.

13 Probably the greatest difficulty of some of those who preceded Mendel and who almost attained his results was that they could not see the forest because of the trees. The data obscured the laws.

14 An amusing feature of the criticisms of the biometric school by Mendelians is the fact that the critics have failed to realize that the features of both methods of approach which are of the greatest importance in science are the same — namely, the replacement of the confusing irregularities of empirical frequency distributions by the illuminating regularity of mathematical expressions which represent the results with a degree of accuracy which lies within the limits of the probable errors of random sampling.

degree of interrelationship between the variables with which we have to deal. His conception of correlation and regression, vastly extended and enriched by Pearson of the Biometric School, has given us some of the most powerful tools in biological research.

There is no time at my disposal for a history of biometry, nor is this the occasion for an indication of what biometry has accomplished or what it is capable of accomplishing for biology in the future. It is sufficient for the moment to point out that many thoughtful biologists recognize the fact that the progress of science depends not merely upon the accuracy of measurement and the closeness of control of experimental conditions, but upon the adequacy of the mathematical description and analysis of the observational, assembled toward the solution of a given problem. This was not obvious in Galton's day. He foresaw in part the long and bitter fight which would be necessary to establish mathematical analysis as an essential part of biological investigation, but the campaign fell to the lot of younger men. It is to his glory to have had the vision. It has been the opportunity and the privilege of his followers to wage the battle.

XIII

In many of the comparisons hitherto drawn there is some element of parallelism, however approximate; some semblance of equality, however slight, between the achievements and the influence of Mendel and Galton. When we turn to Galton's greatest potential contribution of human advancement there is no possibility of comparison further than to note the significant fact that it was not the ecclesiastic, Mendel, but it was the biologist, Galton, who had the vision to foresee the possibilities of the improvement of human stocks under present conditions of law and sentiment.

Thus what may become the most fundamental service of science to humanity was not foreseen, or at least not formulated or fostered by one whose vocation was religion but by one whose vocation was science.

Nor was it merely a question of vision. Galton not only foresaw[15] the possibilities of the application of the laws of biological science to

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15 It is an interesting fact that in his first paper on inheritance (1865) Galton wrote: "The power of man over animal life, in producing whatever variety of form he pleases, is extraordinarily great. It would seem as though the physical structure of future generations was almost as plastic as clay, under control of the breeders' will. It is my desire to show, more pointedly than — so far as I am aware — has been attempted before, that mental qualities are equally under control" (p. 157). On another page of the same essay we read: "I hence conclude that the improvement of the breed of mankind is no insuperable difficulty. If everybody were to agree upon the race of man being a matter of the very utmost importance, and if the theory of the hereditary transmission of qualities in men were as thoroughly understood as it

the improvement of human stocks, but he had the energy, courage and practical wisdom to make such provision as he could for the realization of his vision. He himself contributed extensively to the research[16] which should precede propaganda[17] and must precede legislation or action. His contribution was not merely the products of his own pen, but the personality drew about him a school whose researches contributed to the advancement of the science in which he was interested as rapidly as the care which such work demands made progress possible. Finally, he provided that the major portion of his private fortune should be devoted to the foundation of the first laboratory for national eugenics, and named as his personal choice for its head one of the ablest and most productive scientific men of our generation.

This is neither the place nor the time to discuss in detail the work of the Galton Laboratory, where the highest ideals of rigorous investigation have been steadfastly maintained, or the status of eugenics as a science. It is enough to say that the interest engendered by the pioneer work of Galton, vigorously forwarded at a later date by the work of Karl Pearson and by the establishment of the Galton Laboratory, has been the direct cause for the establishment of a series of similar institutions throughout the world.

Finally, let us say to the credit of Galton himself that while his earlier writings were too far in advance of their time to receive serious consideration he did not succumb to discouragement. In the later years of his life he might have been the hero of a mob of enthusiasts, but he was willing to be patient and to wait for research to lay the needful foundations.

XIV

Which was the greater man? Which has influenced most profoundly the development of science as we know it to-day? Which has set in motion the more important forces for the future development of science?

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is in the case of our domestic animals, I see no absurdity in supposing that, in some way or other, the improvement would be carried into effect."

16 Galton's chief volumes have been cited above. It would lead us too far from our purpose to attempt to cite or review the minor papers which show the development of his interest in and appreciation of the problems of eugenics.

17 Galton was aware of the dangers of propaganda. Thirteen years ago, when some of his essays were assembled in a little volume, "Essays on Eugenics," by the Eugenics Education Society, he wrote in the preface: "It is above all things needful for the progress of eugenics that its advocates should move discreetly and claim no more efficacy on its behalf than the future will confirm; otherwise a reaction will be invited."

Personally, I have no shadow of doubt as to the correct answers, but I shall not obtrude my own opinion upon you.

After all, the questions do not demand formal answers. Let us instead content ourselves by repeating a sentence from our introductory remarks: “Both men worked in advance of the science of their own generation. Both have influenced in a profound and far-reaching manner the science of subsequent generations.”

It is fitting that the American Society of Naturalists should do them honor.

Shull, G. H. 1923. A permanent memorial to Galton and Mendel. *The Scientific Monthly*, 16: 263-270.

A PERMANENT MEMORIAL TO GALTON AND MENDEL

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When the Mendelian principles of heredity were simultaneously rediscovered and promulgated in 1900 by de Vries, Correns and Tschermak, the systematic study of variation and heredity had been already for several years proceeding with vigor along a wholly different line, known as biometry. As increasing numbers of zealous workers in the Mendelian field made it increasingly evident that the principles discovered by Mendel had widespread if not general validity, the inevitable conflict between the Galton-Pearson methods of attack on the problems of genetics and the Mendelian methods engendered much bitterness and even as late as 1909 an "Ardent Mendelian" depicted the devotees of biometry and those of Mendelism as two armies pitted against each other in mortal combat with ultimate victory inevitable for the Mendelians. We can not admit that this picture ever accurately represented the attitude of biometricians or of Mendelians, generally, though in individual cases it may perhaps have been justified.

What a change hath the past decade wrought! With keen satisfaction we bracket together to-day the names of Galton and Mendel with the assurance that in so doing we give offense to no one! *Mendelism has indeed won the victory, but so also has biometry!* And instead of mortal combat, there has come fraternization, mutual understanding, cooperation, even amalgamation, so that to-day the names of Galton and Mendel stand as twin pillars in the basement room of the house of modern biology, which has been christened "Genetics."

To geneticists it is well known that the fundamental concept in both biometry and Mendelian heredity is one and the same concept; to other biologists this may not have been fully appreciated as yet. Both biometry and Mendelian heredity involve the amassing and analysis of statistics, and the analysis in both rests on the assumption of independent assorting of pairs of alternatives. The basic principle of both is the principle known as the "law of chance," a principle which might be less easily misconstrued if it were always spoken of as the "law of probability," since the word "chance" connotes to many the antithesis of causation whereas in reality it assumes that even events which are individually unpredictable are due to the interplay of definite causes. The simplest phase of this principle may be represented by the repeated tossing of a coin which may fall either "head" or "tail." Cases of increasing complexity may be as simply illustrated by the repeated tossing of two coins at a time, then 3 coins at a time, 4 coins at a time, and so on, to any degree of complexity desired. Mathematically, the results are symbolized by the expression $(a+b)^n$ in which a and b may each be assumed to have the value unity. Mendelian phenomena, as practically handled, usually involve only the lower values of n in this formula (the number of allelomorphic pairs) and also generally require that a and b be of such character or magnitude that they may be easily distinguished from each other. Biometry, on the other hand, works ideally with cases in which n is large, and the alternatives represented by a and b are not easily or not at all differentiable. But there is no *natural* line of distinction between cases in which n is small and those in which it is large, nor between the cases in which a and b are easily distinguished and those in which they are not easily or not at all capable of distinction. The combination of biometry and Mendelism in modern genetics has resulted therefore quite naturally from extended experience in both fields with mutual invasion and overlapping.

The significance for modern biology of the introduction of statistical methods has been well discussed by the last preceding speaker and I will attempt to add nothing to this; but rather take occasion to point out a certain interesting parallel and antithesis in the lives of the two men the centenaries of whose births we celebrate to-day.

Not only were Galton and Mendel born in the same year (1822), but they also published their first scientific contributions at nearly the same time, and at a time that must be considered in these days relatively late in life, namely the age of 43. Mendel's classic paper was read in 1865 and printed in 1866, while Galton's first papers on the statistical study of heredity were published in *MacMillan's Magazine*, in June and August, 1865, but the existence of these would be now as completely buried in oblivion as was Mendel's paper before the "rediscovery" were it not that they were mentioned by Galton in a book that has lived, entitled "Hereditary Genius," published in 1869.

Aside from the coincidence of these two cardinal dates (their births and the dates of their first publications) in the lives of Galton and Mendel, their biographies are much more striking in their strong contrasts than in their parallelism; for Mendel was the son of a peasant, while Galton was born to a family already well endowed with the results of several generations of energetic commercial life and thrift. Mendel continued but a short time in the execution of genetical experiments after the publication of his greatest paper; Galton continued his studies throughout a long life and contributed books and magazine articles almost to the day of his death, and in his will he endowed a laboratory to continue in perpetuity the type of research which he had inaugurated. Mendel died in 1884 at the age of 62, wholly unknown to the scientific world; Galton, on the other hand, died in 1911 at the ripe age of almost 89 years, and was well laden with the various honors which admiring scientific and governmental organizations could bestow.

There is something fine in the spontaneity which has been shown by scientific organizations, both national and international, in taking cognizance of this centennial year. All the genetical journals and a number of other biological journals have celebrated in one form or another, and several special commemorative programs have been arranged. The most notable of these was the international gathering in Brünn, Czechoslovakia, in September last.

It is to be noted, however, that these various activities represent quite ephemeral manifestations of the great respect and admiration we all feel for Galton and Mendel. The question has been raised whether these sentiments ought not to be expressed in some more enduring form, and the answer has seemed to be inevitably in the affirmative; but what should be the nature of such a memorial?

Tablets of bronze, and busts or statuary of bronze or marble, appropriate locally to mark the places of birth or of labor, are hardly appropriate for us who have in our midst no *places* to thus commemorate in association with the names of these two great spirits. There is left, however, an even better association than that between name and place, to which to attach a memorial, namely, the association between the men and the *work* to which they gave their devotion and which laid the foundations of a new branch of biological science. It is suggested, therefore, that the best type of memorial is one which will, in perpetuity, promote the sort of scientific activities to which they were devoted.

It is a fact now well known in scientific circles that the research journals are in difficulty, and unable to meet the current needs of research men for the recording and promulgation of their discoveries. It is recognized that this condition seriously menaces rapid progress in scientific discovery. *Genetics,* particularly, has been unable to meet the needs of geneticists who work with color characters, nor has it been able without special gifts either from the authors themselves, or from other outside sources, to publish the expensive tabular matter required in a statistical science. It will be recalled that in Mendel's original study, four of the eight alternative characters which he considered in the garden pea were color characters, and modern geneticists have likewise found pigmentation characters forming a considerable portion of their most instructive research material. Gross verbal descriptions of such pigmentation characters serve fairly well the crude preliminary studies, but as the analyses become sharper and more detailed such verbal descriptions are certain to lose much of their value. It is proposed therefore as a permanent memorial to the founders of the science of genetics to ask for popular subscriptions to a "Galton and Mendel Memorial Fund" the principal of which shall be kept invested in perpetuity, the income from which shall be devoted to the publication of such colored plates and other expensive types of engraving as may be necessary in the illustration of research papers in the journal *Genetics,* and also to defraying in part the cost of publishing necessary tables of statistics.

There is a special reason why this is a particularly appropriate type of memorial for Gregor Mendel. Several suggested explanations have been offered to account for the long submergence of Mendel's magnificent contribution, and all such explanations doubtless have a certain degree of validity, but the explanation which seems most generally acceptable is that of defective publication. It is true that the *Transactions* of the Natural History Society of Brünn were being exchanged with no less than 120 other societies and institutions of similar scope or related purpose; but it is hardly to be doubted that had his paper been published in one of the standard biological periodicals of the day it would not have remained for 35 years unknown to others capable of appreciating its bearing.

The significance of the type of memorial here proposed will become clearer when we consider what becomes of the papers which can not be published in any of our standard journals because of the need for expensive types of illustration, or for unusual quantities of tabular matter. Some American papers requiring colored plates have been sent to England or Germany and published in foreign journals; but it is obvious that these sources of publication facilities are strictly limited. Probably the greatest number are published without the illustrations and tabulations required for the full realization of their value. A number of papers with colored plates or other expensive engravings have been published as University Bulletins, the method of issue of which is similar to that of Mendel's original paper, and for this reason they may be expected to be less readily accessible as the years go by than if published in a standard journal like *Genetics*. Have we any assurance that we are not burying in this way to-day important contributions which may or may not be rediscovered, several decades hence?

The amount of money needed to meet present requirements of illustration and tabular matter in *Genetics* has been estimated at $50,000 and this sum is therefore set as the goal to be aimed at.

Is it not clear that since the contributions of Galton and Mendel and the science which they founded touch vitally every branch of biology, giving new viewpoints and new outlook, it is proper to invite all biologists and all those interested in the applications of biology to cooperate in the establishment of this Memorial Fund?

A considerable number of contributions ranging from ten to one hundred dollars each have been received already from biologists, as well as from others who, though not biologists themselves, have an interest in the progress of biological discovery. Since it will be impossible to appeal by individual letters to all of the thousands of biologists in the country, each reader who has not already sent a donation is asked to consider this a direct personal appeal for a contribution to the Memorial Fund. The fund will have its proper character as a memorial only if (or in proportion as) the list of donors contains the names of all who understand and appreciate the epoch-making work of Galton and Mendel.

A permanent list of donors will be kept in which the following grades will be maintained: Persons contributing $5,000 or more will be designated Founders; those giving $1,000 or more, Patrons; $100 or more, Supporters; $10 or more, Contributors; and those who give less than $10 will be listed as Associates.

Checks or other valuable securities, such as stocks or bonds, should be made payable to the Galton and Mendel Memorial Fund and sent to the Secretary of the Editorial Board of *Genetics*, George H. Shull, 60 Jefferson Road, Princeton, New Jersey, who will render prompt acknowledgment.

The permanence of the memorial will be insured by placing the fund in the hands of a conservative Trust Company, and only the income will be used as needed for the purposes stated. Formal acknowledgment will be made whenever any part of this income is used, and provision will be made also that in the event that it can be no longer appropriately used in the manner here designated the fund will pass to the trusteeship of the American Association for the Advancement of Science for reallocation in such manner as will in its judgment best serve as a memorial to Galton and Mendel.

It is believed that this very practical type of memorial will meet the approval of all those who realize that the best memorial to a scientist is one which serves to promote the work in which he was interested. It is also believed that biologists will generally esteem it a privilege to enroll themselves among the admirers of these two great prophets of modern biology — Francis Galton and Gregor Mendel.