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Electronic Scholarly Publishing Project

Foundations Series: Classical Genetics

Series Editor: Robert J. Robbins

The ESP Foundations of Classical Genetics project has received support from the ELSI component of the United States Department of Energy Human Genome Project. ESP also welcomes help from volunteers and collaborators, who recommend works for publication, provide access to original materials, and assist with technical and production work. If you are interested in volunteering, or are otherwise interested in the project, contact the series editor: rrobbins@fhcrc.org.

Bibliographical Note

This ESP edition, first electronically published in 2000, is a newly typeset, unabridged version, based on the original 1936 edition published by United States Department of Agriculture. Unless explicitly noted, all footnotes and endnotes are as they appeared in the original work. The figure on page 22 is a bitmap image of the figure in the original.

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IN ATTEMPTING TO BUDGET OUR DISCUSSION I find there is apportioned about one minute of talk for each year of research in our quarter century of genetics progress. I figure there were about 1000 geneticists who took part in the Fifth International Congress of Genetics at Berlin in 1927 and nearly as many were in attendance at the Ithaca Congress in the depression year 1932. A conservative estimate of the geneticists in the world during our period indicates that a pro rata distribution of time would allow 0.7 second to discuss one year's work of 25 geneticists or 25 years' work of a single geneticist. Seven tenths of a second is about the time necessary to pronounce the word "Genetics." You will appreciate my embarrassment, therefore, when I confess that my personal interest in genetics began about the year 1910, which is the starting point of our 25 year period under discussion. If I take more time to speak of the work with which my colleagues or I have been connected than would be necessary to say the word "genetics" it is only because it seems safer in such a large field to take my examples from work that is most familiar.

We often hear the expression "Leaders of Science." As a matter of fact so-called leaders often lead less than they are pushed. It is not the conspicuous spray which erodes the coast line of our continents but masses of water which surge forward with united front. We may change the figure and say that the advancement of science is like that of an amoeba – a mass movement with individual projections extending only a slight distance beyond the advancing edge. It is for this reason that so frequently important discoveries have been made independently at about the same time, as was the case with the rediscovery of Mendel's law. Mendel communicated his discoveries to Naegeli, an acknowledged leader in heredity and his published paper was cited in Focke's Cyclopedia of Hybridization in 1887. Some have thought that if Darwin had known of Mendel's work this important generalization would not have lain unnoticed for over 30 years. Darwin, however, made a cross between a peloric and a normal snapdragon *(Antirrhinum)* which gave a 3:1 ratio in the second generation without realizing the significance of this segregation. We are forced to conclude that Mendel was an offshoot so far removed from the main body of thought of his time that he had no conspicuous influence in the advancement of biology, either then or now. It was the independent experiments of three investigators which led to the rediscovery of Mendelism in 1900 and it is the influence of 1900 which is felt today and not that of 1866 when Mendel announced his discoveries in the proceedings of the Naturforschender Verein of Brün.

The history of genetics may be divided into the ancient and the modern. The ancient history includes the early hybridizers from the time of Camerarius, 1690, to Darwin's "Origin of Species" in 1859 and the period that may be called the Age of Darwin from 1859 to 1900. This latter was an age of species and speculation. New ideas bring at first freedom but later bondage. And so the idea of evolution at first stimulated speculation but later stifled experimentation. The return to experimentation ushered in the modern period. This also may be divided into two parts. The period from 1900 to 1910 may be called "Mendelism and 3:1 Ratios" while the period from 1910 to the present may be labeled "Brass Tacks, – Genes and Chromosomes."

The early hybridizers were practically all botanists. I need mention only Camerarius, Koelreuter, Gärtner, Godron, Naudin and Darwin, who in experimental work would rank as a botanist. It was no accident that Mendel's law was first discovered through study of a plant, the garden pea, nor that this same law was independently discovered by three botanists, de Vries, Correns, and Tschermak, through their experiments with plants. Nineteen hundred was the birth year of modern genetics. Bateson became an early champion of the new science. He began his scientific life as a zoologist but largely reformed and became a botanist using plants as the chief objects of investigation and becoming director of the John Innes Horticultural Institution. The botanist, de Vries, early gave us the mutation theory and started a pack of botanical hounds on the eager trail after new forms of the Evening Primrose. A botanist, Johannsen, gave us the pure line theory – distinguishing what organisms appear to be (phenotypes) from what they actually are in hereditary constitution (genotypes). It is true that in this early modern period there were some zoological geneticists. The English school under the leadership of Bateson had worked on poultry as had also Davenport in this country. Cuénot in France had worked on mice and Castle had worked on rats and rabbits. Up to 1910, however, genetic investigations had been almost exclusively in the field of botany.

It was in 1910, or thereabouts, that the little yeast fly, *Drosophila,* was found to be an organism adapted to the study of mutations and Mendelian heredity, and a new era in genetics was inaugurated. The idea of using *Drosophila,* like most good ideas, had an evolution. An outline of this history can be given from personal communications from Drs. Castle, Lutz, and Morgan. In 1900 Castle was looking around for material that could be bred in quantity for study of heredity in addition to rats, mice, and guinea pigs which he was then using. Professor C. W. Woodworth, an entomologist from the University of California, who was in Castle's laboratory raising *Drosophila* on fermenting grapes in a study of an embryological problem, suggested the availability of these little flies. After the season for Concord grapes was past, they tried other fruits and finally settled on bananas which remained the standard *Drosophila* medium for many years. It was later discovered that what the larvae really eat is the yeast and not the fruit and in consequence methods of cultivation have been greatly simplified. From 1900 to 1906 Castle and his students carried on experiments with *Drosophila* chiefly to discover the effects of continuous inbreeding. Around 1905 or '06 at the suggestion of Castle, W. J. Moenkhaus began to breed *Drosophila* in an attempt to alter the sex ratio genetically. Some of his work was carried on at Cold Spring Harbor. F. E. Lutz was working in Cold Spring Harbor at this time at the Station for Experimental Evolution of the Carnegie Institution of Washington and following the example of Moenkhaus took up the breeding of *Drosophila.* In the spring of 1907 he had under way a selection experiment on abnormal wing venation. A white-eyed *Drosophila* was found among some dead material, but this single variation was not further investigated due to the program of work on wing venation. A little later T. H. Morgan began looking around for available material for genetic work at Columbia where, very fortunately as it turned out, there were no funds for raising larger animals. Knowing of the other work on *Drosophila,* he tried out this animal which costs a laboratory so little for board and lodging, bringing in material from outside as well as getting cultures from Lutz.

The science of genetics may be congratulated that the Columbia budget was meager in the days preceding our 25 year period, but the availability of *Drosophila* had already been established and other laboratories soon would have been using *Drosophila* in high pressure genetic studies if the Columbia laboratories had been wealthy and taken to breeding such an expensive and genetically undesirable animal as the elephant.

It may be of interest in this connection to mention a dozen organisms which have been used rather extensively as genetic reagents, listing them according to the number of gene types. Maize (our American corn) must be mentioned first with about 250 known genes. The snapdragon *(Antirrhinum)* is next with about 200 known genes followed by the Japanese morning glory *(Pharbitis Nil)* with about 110 and the garden pea with about 100. The sweet pea has about 20 known genes. In *Datura* we have about 40 genes which have been located in the proper chromosome and about 200 or more others that we are calling genes but which we have not yet located. In animals we have in the domestic fowl, according to D. C. Warren, from 40 to 50 known genes. In the mouse there are around 25. In the rabbit, according to Castle, the identified genes number 16 located in 12 different chromosomes. In man, according to Davenport, it is safe to say there are not more than 25 to 50 genes that can be spoken of as known in the sense in which genes are said to be known in the other forms in our list. In *Drosophila melanogaster* there are 500 to 600 known genes not counting genes identified in several other species of *Drosophila.* In the parasitic wasp, *Habrobracon,* about 75 genes have been identified. Among plants, the Japanese morning glory is the only organism of much importance from the standpoint of the number of its known genes which had not been studied genetically before the beginning of our 25 year period. Among animals, the chief new organisms of genetic study are *Habrobracon* and certain species of *Drosophila. D. melanogaster,* as we have seen, had been studied considerably in the first part of our modern period. The difference between a good and a bad living reagent for genetic investigations may be seen by comparing man, the worst, with *Drosophila,* the best genetic “Versuchsthier,” in respect only to rapidity of breeding (30 generations for *Drosophila* in a year) and the cost of cultivation. Proper techniques and proper living reagents are as important for research in biology as are techniques and reagents in research in physics and chemistry.

I have called the first decade of the present century the period of Mendelism and 3:1 ratios. This was a period of stock taking. Many characters had been found to Mendelize and give 3:1 ratios in the second generation, but it was still an open question how much of inheritance followed Mendel's law. Mendelian or "mosaic" inheritance was contrasted with blending inheritance. In a symposium on Botanic Gardens before the American Association for the Advancement of Science published in 1910 I spoke of plans to have both types of inheritance represented in the Agricultural Botanic Garden at the Connecticut State College. The Jimson Weed was used to illustrate mosaic inheritance but I remember having trouble in finding a good example of blending inheritance and East, whom I recollect consulting, could not help me out. The work since 1910 has changed the question so now we ask if there is any inheritance which is not Mendelian. Though some still claim there may be inheritance of a kind through the cytoplasm, the presumption is that if transmission from one generation to the next is not through the mechanism of genes and chromosomes, it is not to be called inheritance at all.

Since 1910 the field of genetic research has broadened both in respect to types of organisms and in respect to the structures and processes investigated. Throughout the plant and animal kingdoms the method of inheritance has been found to be essentially the same, a fact which emphasizes the unity of living things. In the botanical field genetic study has been extended to the cryptogams. I need mention only the work of Dodge on the fungus *Neurospora* and that of Allen on liverworts. Mosses and ferns and even the smuts also can now be used to illustrate Mendel's law.

Genes have been identified which affect practically all parts and processes of the plant from early embryo to late fruit. Resistance and susceptibility to disease, the pH of the cell sap, the size of chromosomes, the self sterility of flowers have all been shown to be conditioned by known genes. In *Datura,* for example, we have found a gene responsible for failure of chromosomes to pair at reduction, the behavior of which has been worked out by Dr. Bergner; a gene which Miss Satin has investigated causes doubling of chromosomes; several genes responsible for abortion of pollen grains at different stages of development studied by Cartledge; and several genes also for abnormalities in pollen-tube behavior disclosed by the studies of Buchholz. Sinnott has shown that a single gene may cause profound changes in the anatomical structure both internal and external and Avery and the speaker have located genes which have such diverse effects as production of male sterility, reduction in size of flower, complete elimination of purple pigment or its restriction to parts of stem below the cotyledons and various defects in chlorophyll production. We may classify the different types of genes according to their method of action rather than according to the specific part or process which they affect. Thus we speak of complementary, multiple, duplicate, modifying, quantitative, and lethal factors. Genes may be trivial or important in their effects upon the organism. Naturally the geneticist who wishes characters as markers with which to follow the behavior of chromosomes in which their genes are located prefers those characters like floral colors which least disturb the life of the organism. It can no longer be said, however, that Mendelism has to do only with unimportant characters.

Timoféeff-Ressovsky has made a tabulation of genes according to their effect upon the viability of *Drosophila*. To every gene causing a visible effect he finds there are four genes that are lethal, that is which kill the organism, and ten genes which are sublethal, that is which reduce slightly the viability without killing the organism and with only a slight, if any, visible effect. Mutations with slight visible effects are most numerous. We seem thus to be getting back to Darwin's small fluctuating variations except that now we distinguish genetic from environmental causes of variation.

In the early days of genetics, we used to speak of unit characters as if each adult characteristic were caused by a single unit factor. We still speak of unit factors but no longer of unit characters. We now realize that there is an interaction of factors with each factor influencing more or less strongly the expression of all other factors. It has been shown, for example, that for the normal development of chlorophyll in maize the interaction of at least 65 factors is necessary. We now speak of chromosomal balance and of genic balance.

Our quarter century, 1910-1935, I have labeled "Brass Tacks, – Genes and Chromosomes" because it has been during this period we have come to realize that it is possible to get down to brass tacks in genetics and that these brass tacks are the genes and chromosomes. In 1906 at the British Association for Advancement of Science I heard a symposium on what, if any, relation there is between heredity and chromosomes. The relation is now recognized as a simple one, – that of cause and effect. Bateson, who was such a valiant crusader and effective defender of the faith in Mendelism during the first decade of our century when the new teachings were attacked by biometrical opponents, never fully accepted chromosomes as a mechanism of heredity. At the Toronto meeting of the American Association for the Advancement of Science in 1921, he made public confession of his conversion to belief in chromosomes, but he never came to think in terms of chromosome behavior.

It will be possible to outline only some of the more important new principles established in the last 25 years. In doing so it will be noted that these discoveries must be described in terms of chromosomes and their constituent genes.

First may be mentioned linkage and the linear order of the genes established in *Drosophila* through crossing-over values. It is true that Bateson and Punnett had earlier discovered linkage and breaks in linkage in the sweet pea, but they had called this coupling and repulsion and had explained the phenomenon by an hypothesis of differential rates of division of cells preceding the formation of gametes.

An important discovery in the latter part of our period was that like parts of chromosomes are together at reduction and that the attachments of known chromosomes may be used to identify the ends of unknown chromosomes. Belling used this method effectively in interpreting heteroploid types in *Datura* and with it worked out the important discovery of segmental interchange which is a process of chromosomal rearrangement not uncommon in nature. Simple translocations in which a part of a chromosome has become permanently joined to a non-homologous chromosome had been discovered in *Drosophila* in the earlier part of our period.

The study of heteroploidy is a development chiefly of the last 25 years. It is true that heteroploidy of different kinds was found in *Oenothera* before our period began but the tendency was to consider the extra chromosomes as a characteristic rather than as a cause of the mutant types in this genus. The mutations in *Oenothera* responsible for "elementary species" were thought by de Vries and his immediate followers to involve the formation of new hereditary units. We now classify them not as gene but as chromosomal mutations and explain their effects as due to a change in chromosomal balance. At one time *Oenothera* appeared to be an anomalous genus in its hereditary behavior with little bearing on the genetics of other groups. Due to three major discoveries made within our period, – Muller's balanced lethals, Cleland's association of chromosomes in circles, and Belling's segmental interchange, the breeding behavior in *Oenothera* is becoming better understood and other forms are being found to exhibit similar phenomena.

Unfortunately time will not permit a further discussion of heteroploidy which is a subject of more importance in Botany than in Zoology. I should like to point out the value of 2n + 1 types in an analysis of the factorial constitution of unaltered chromosomes and the use of trisomic ratios in locating genes in maize as well as in *Datura.* Search for information about chromosomes has led to investigation of their intimate behavior in the early thin thread stages. For example, valuable information has been obtained in maize, notably by McClintock, regarding the pairing of chromosomes in these early stages. What actually happens at the time of crossing over in the chromatids and the function of chiasmata is still a question debated by Darlington, Sax, and others.

The search is being extended to still further recesses of the chromosomes and investigators such as Demerec are studying the very nature of the gene itself which was once considered only an imaginary concept like the equator which we may sail over in the tropics without feeling any bump.

Among the important advances in the last 25 years should be mentioned three techniques. The aceto-carmine method holds among techniques the position that *Drosophila* holds among "Versuchsthiere." It has enabled studies to be carried on with large numbers that would not have been possible with sectioned material. Belling's contribution to the technique was the addition of iron which left the cytoplasm clear. Other modifications have been made by different investigators but he was the first who used it extensively in cytogenetic work.

The second technique to be mentioned is the induction of mutations by radiation treatment. The chief credit for this discovery properly belongs to Muller but like most discoveries there is considerable history back of it. The desire to control the type of offspring is earlier than modern genetics. You remember the account in Genesis, dated B.C. 1747 in biblical terminology, which described Jacob's method of increasing the proportion of spotted lambs, which were his share of his father-in-law's flock, by exposing peeled rods before the ewes at time of mating. More nearly in our present period is the suggestion made by de Vries in an address in 1904 at the dedication of the Station for Experimental Evolution. He urged that the rays of Roentgen and Curie, which are able to penetrate into the interior of living cells, be used in an attempt to alter the hereditary particles in the germ cells.

In the beginning of our period Loeb and Bancroft, with the assistance of Bagg, used x-rays, radium, and high temperatures in an attempt to induce mutations in *Drosophila.* Some mutants were obtained but there is no clear evidence that they were not already in the stock when the treatments were started. It is also probable that the mutants later obtained in mice by Little and Bagg, some generations after treatment with x-rays, were homozygous extractives of genes already present in the stock. Morgan early carried on some work in treating *Drosophila* with radium, with the result that some of the descendants of the treated flies produced mutants of the ordinary type. The work was not followed up apparently because the numbers of mutants were small and the effects not specific. Mavor later obtained definite effects of radiation upon crossing-over and non-disjunction, and Gager, in cooperation with the speaker, in a single experiment with radium emanation obtained an increase in non-disjunctional types and a couple of recessives out of a number so small as not to be surely significant statistically. After Muller had announced the results of his well planned experiments it was discovered that both Stadler and Goodspeed had radiation experiments under way which later gave them an abundance of induced mutations. I need only mention here the induction of mutations by heat treatment, in which Muller also led the way, and the very recent discovery by Navashin, which has been energetically followed up by Cartledge, that merely aging seeds on laboratory shelf will increase their mutation rate. The ability to obtain at will an abundance of both chromosomal and gene mutations has been of tremendous value to experimental genetics and has made it possible to subject the process of mutation itself to experimental study.

The third technique of which it seems desirable to speak is so new that it is difficult to appraise its full value. The discovery that the structures in salivary glands of the larvae of flies are in fact chromosomes with markings corresponding to the gene loci appears to have almost staggering possibilities in the way of permitting an accurate analysis of chromosomal structure hitherto impossible. Imagine for a moment, an astronomer who has been studying the planet Mars and trying by enlarging the telescopic lens and increasing the sensitivity of the emulsion on the photographic plate to learn more of the structure of this heavenly body. He may feel that he has about reached the limits of increased vision by changes in telescope and photographic plate but in his wildest dream he probably never imagined he could induce the planet itself to grow bigger so it could be seen more clearly. This, however, is just the kind of a thing that has happened to the salivary chromosomes. They have swollen up not two or three times the usual size we are accustomed to but 100 and 150 and even 170 times the size of chromosomes in other parts of the fly. All the markings, which are being found to have so much significance, have swelled up from invisibility into visibility so that we can now count and chart them and determine their relation to our ultimate units, the genes. This like most other discoveries also has a history. Painter appears to be the one to be credited with realizing that the salivary structures were chromosomes with markings capable of being related to genes. Heitz independently, and in fact earlier, pointed out that the banding in the salivary chromosomes is a constant characteristic. Many others, some even in genetic laboratories, had figured them without sensing their significance in genetic research. Bridges and Koltzoff independently interpreted the salivary chromosomes as compound structures, consisting of two cables of many chromosomal strands. Bridges has given detailed drawings of the four salivary chromosomes of *Drosophila melanogaster* with a reference system for their markings which is being used by many workers in this new field.

It is interesting to note to what extent the study of evolution was restricted by the experimental work in genetics. It is only within the last few years that the methods used in genetics have been actively applied in an attack on evolutionary problems. Bateson in his Toronto address in 1921 despaired of genetics being able to offer any help toward a solution of the species problem. At that time, however, English botanists had already made discoveries in the behavior of chromosomes of *Primula Kewensis* which offered a clue to a method of species formation. In study of the species problem more progress has been made with plants than with animals. The differences between species have been studied by means of an examination of chromosomes of hybrids in *Oenothera, Viola, Crepis, Nicotiana, Datura,* and other genera. The conclusion is being reached that the problem of evolution of species may most profitably be investigated in terms of the evolution of their chromosomes. It is seen that blocks of chromosomal material with their genes can be readily shifted from one chromosome to another. Many of us have felt the inadequacy in accounting for the origin of new species by the mutation of single genes one at a time and have looked rather for differences involving whole blocks of genes. It was with considerable satisfaction, therefore, that we learned that the salivary chromosomes in *Drosophila* show reduplicated areas in the chromosomes and thus give support to the idea of evolution by change in chromosomal balance. Experiments in the greenhouse and garden have given clues to what is found in nature. In the sterile hybrid form of *Primula Kewensis,* the chromosomes from the two parents, *P. floribunda* and *P. verticillata,* are unlike and hence have difficulty in pairing with each other in reduction divisions. When doubling of all the chromosomes of the sterile hybrid had taken place to form the "amphidiploid" fertile *P. Kewensis,* the chromosomes derived from each of the parent species had homologues with which they paired and a new pure-breeding species with a new balance was developed. Many other examples of the origin of amphidiploids under controlled conditions could be given and pure-breeding new types have been synthesized in *Datura* by addition of blocks of extra chromosomal material. By proper breeding manipulation of the chromosomes Müntzing appears to have duplicated a species, *Galeopsis Tetrahit,* found in nature.

In the early days of Mendelism much was heard of the presence and absence hypothesis which taught that the dominant character is represented by the presence of something material, whereas its allelomorphic recessive is due to the loss of this dominant gene. The presence and absence hypothesis has been abandoned as an explanation of genes in general but it is interesting to note that in *Drosophila* and maize detailed study of chromosomes in connection with breeding behavior has demonstrated that sometimes genes may be lost without lethal effect and in such cases the loss may behave like a recessive. It is not always easy to distinguish effects due to genes from those due to chromosomal abnormalities. In *Datura* for example, we have many cases in which blocks of extra chromosomal material behave like dominant genes in inheritance and we have at least one case in which the chromosomal block behaves like a recessive gene in that the heterozygous types are indistinguishable from normals although the homozygotes are readily recognized. The presence and absence hypothesis led Bateson to conclude that evolution must be a loss phenomenon, that man, for example, differs from amoeba in the large number of amoeba genes which man has lost.

Lotsy appears not to have worried greatly about the origin of genes in his attempts to explain all evolution by hybridization. Modern genetics is unable to support Lotsy's extreme views but it is becoming evident that, in plants at least, hybridization in connection with polyploidy has been an important method of evolution. In this connection I need mention only such forms as cultivated wheats in which the chromosome numbers (n=7, 14, and 21) form an arithmetical series and in which evidence is at hand that the types with 21 pairs of chromosomes have a compound chromosomal complement made up of three different groups of chromosomes. Genera such as *Crepis, Carex,* and *Drosophila,* in which the chromosome numbers of different species run more or less consecutively, afford evidence of evolution through major chromosomal changes rather than merely by means of the accumulation of single gene mutations. Polyploidy alone seems not to have played a great role in species formation in nature, though a number of true tetraploids (i.e., with 4 of each kind of chromosome.) exist in the wild as distinct species or races. Among these may be mentioned the 4n species of *Empetrum hermaphroditum* apparently derived from *E. nigrum,* the 4n form of *Tripsacum dactyloides,* and perennial teosinte *(Euchlaena).*

The discoveries in genetics of the last 25 years have changed our viewpoints and through them altered our philosophy of life. I have touched on these matters elsewhere. I need only point out in this connection that a mechanism of heredity has been firmly established and as a consequence certain old problems no longer bother us. We do not believe in telegony, maternal impressions and the inheritance of acquired characters because they go counter to the established mechanisms. Before the mechanisms were known, they seemed reasonable. No geneticist now thinks of any conflict between belief in heredity and belief in environment since he is accustomed to take into consideration the responses of a given gene in different environments, not excluding the internal environments brought about by the interaction of other genes. Perhaps before telling of the wonders of genetics, geneticists can do a service to their own science as well as to their lay friends, who are inclined to take the side of environment as opposed to heredity, by pointing out that life cannot exist without both the proper heredity and the proper environment.

We have said that genetics narrowed the point of view of the student of evolution. Genetics has also had a broadening influence. A geneticist can no longer be a botanist or a zoologist only, since the laws of heredity do not recognize the classification into plants and animals. The subject has an integrating influence relating such subjects as physiology, cytology, anatomy, and taxonomy-in fact all the biological -ologies and -onomies. Its relation to experimental taxonomy is of particular interest since both are concerned with the study of evolution. I need only mention here the work initiated by the late Harvey Hall and still being actively prosecuted in California by the Carnegie Institution's Division of Plant Biology. Turesson's concept of Ecotypes (that the environment moulds forms by selecting out of a highly heterozygous population those genes of most value in the given environment) corrects Bonnier's idea of the direct effect of the environment upon habitat forms and shows how genetics and the experimental method may be of aid to taxonomy.

And now let us take two glances into the future.

1. Our last 25 years have brought us again to the species problem. I believe the study of evolution will become increasingly active. It will differ from Darwin's time in that it will be experimental and analytical. It will resolve itself into a study of the evolution of the brass tacks of genetics – genes and chromosomes.

2. When we have learned the mechanisms of evolution, I believe we shall be able, in ways and to an extent impossible to imagine at the present time, to exercise conscious control of evolution.