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SOME ASPECTS OF EVOLUTION¹

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IN his much-discussed presidential address at the 1914 meeting of the British Association, the great skeptic William Bateson finished with the following sentence: "Somewhat reluctantly and rather from a sense of duty I have devoted most of this address to the evolutionary aspects of genetic research. We can not keep these things out of our heads, as sometimes we wish we could. The outcome, as you will have seen, is negative, destroying much that till lately passed for gospel." This negative standpoint was certainly justified to a certain extent by the results of early Mendelian work, which led more in the direction of evolutionary skepticism than optimism. Almost twenty years have passed since, which have witnessed an unbelievable increase in the knowledge of genetical facts. And whereas, as Bateson says, we can not keep these things, namely, the evolutionary

aspect of genetics, out of our heads, geneticists from time to time like to leave their bottles, breeding cages and seed pans and to review the advances of experimental work in regard to their bearing on problems of evolution. I must confess to have been repeatedly guilty myself of this sin during the past 15 years, with the result that the curve of my deliberations was oscillating between skepticism and optimism and still is doing so. Let me not be misunderstood: not skepticism in regard to evolution, which I regard as a historic fact, as all biologists do; but skepticism and optimism regarding the insight into the means of evolution on the basis of genetic facts.

You all know that the majority of the geneticists are to-day rather optimistic. Genetic experimentation certainly has shown that the sudden changes of the hereditary units, the genes, called mutations occur with sufficient frequency to furnish material for selection; it has shown that in plants at least considerable changes, amounting to the formation of

¹ Paper read at a general meeting of the American Association for the Advancement of Science, in Chicago, June, 1933.

what might be termed new species, may be brought about by the different types of chromosome-arrangements which play such an important rôle in present genetical research; and genetics may rightfully claim to have performed experimental changes of forms into other different ones by means which could be conceived as effectual occasionally also in nature; this is at least true for the plant kingdom, but not for animals. In addition, it has been shown that after all Darwin's theory of selection, if properly applied and based upon the present-day knowledge of what Darwin termed generally variation, is still the best guide to an understanding of some of the ways of evolution. This means that, given a certain frequency of mutations, which produce slight changes in a haphazard way and given the selective action of the environment which wipes out certain mutations and lets pass or even favors others, considerable transformations are possible within the time available for evolution. It is not my intention to enlarge here on this topic, which has been treated repeatedly in recent years by leading geneticists. But I have not been satisfied yet that these groups of facts and conclusions, important as they are, tell us the whole story; and I believe that, especially for the animal kingdom, much work has still to be done before we can see clearly how evolution, which we can observe in its great lines as an actual historic fact, has proceeded in detail. I should like then to discuss a few of the fundamental questions regarding the first steps of evolution in nature, which I met in the course of my own experimental work, and then bring to your attention some facts and lines of thought which might assist a deeper insight into our problem.

When Darwin spoke of the origin of species, the Linnean species seemed to be a rather clear-cut unit. Meanwhile we have recognized the existence of micro-species and of subspecies and racial groups, and if we were to define the units which are meant if we are talking about the origin of species, the difficulties would be found insurmountable. In one taxonomic group, what is called a species is hardly distinguishable from the next species, and in another taxonomic group, the species are more different than genera in the first. In my younger days I was working on the minute histology of the nematode worms *Ascaris lumbricoides* and *megalocephala*. These species, though well known to every zoologist as very much alike, proved to be different practically in every cell of their body. At that time I could have undertaken to determine the species from a single isolated cell of many organs of these worms. Compare with this the almost complete impossibility of distinguishing a lion's and tiger's skeleton, in order to realize the hopeless situation for a proper definition. As a mat-

ter of fact the only case of a taxonomic difference between two forms, which can be properly defined, is the difference between a homozygous strain of an animal or plant and one of its mutations. Then, if we are talking about the formation of species, what we actually mean is the origin of very different forms within a group, without consideration of their taxonomic designation as species, genera or even families, which more or less depends upon the personal judgment of the taxonomist.

The majority of the geneticist's work is done with domestic animals and plants or with such wild forms as have given plenty of mutations under cultivation. The obvious reason is that natural species or still more distant units are either sterile *inter se* or produce sterile hybrids and therefore do not lend themselves to the methods of genetic analysis by hybridization.

There is only one taxonomic category about which genetic research has given us proper information: This is the so-called Rassenkreis, a conception which in some taxonomic groups, as birds and mollusks, is gradually replacing the species concept. A Rassenkreis is a series of typically different forms or subspecies found at different points within the geographic range of a species and often showing a typical order of their characters if arranged geographically. As the end members of such a group might be rather different, the idea has arisen that the formation of a geographic Rassenkreis is the beginning of speciation. The idea is that distant members of such a group become finally isolated and will come under the influence of new selective agencies, which carry the stream of further mutational changes into new directions towards the formation of new species and genera. Further, whereas it is found that the differential characters of these subspecies may have adaptational value, it is frequently reasoned that the influence of the environment has produced these forms. To quote only one prominent witness: Henry Fairfield Osborn in a recent address has stood up most emphatically in favor of such views. He writes:

. . . the Buffon-St. Hilaire principle of direct environmental action both on body and germ is now universally admitted as one of the great causes of evolution. As shown in the experiments of Sumner it is directly responsible for speciation in animals like *Peromyscus* (a deer mouse). Sumner has positively demonstrated that modifications in color and form and proportion traceable to the prolonged direct action of environment, are hereditary and therefore true germinal characters. Perhaps the best established zoological generalization of modern times is that subspeciation, and ultimately full speciation is the inevitable result of prolonged change of environment. . . .

I am sorry to say that I can not agree with the eminent paleontologist, either in regard to the evolutionary nature of subspecies or in regard to the origin of their adaptational traits. Simultaneously, with Sumner's work on *Peromyscus* I have analyzed the case of the geographic variation of the gipsy-moth *Lymantria dispar*, and owing to the great regularity of behavior of these geographic races in respect to climatic conditions and also to the possibility of working with large numbers, I was able to make what I believe to be the most complete genetic analysis of a Rassenkreis. As a matter of fact, where Sumner's and my work is comparable the results are also identical, as far as facts are concerned. And I would do injustice to Sumner if I would not state that in his last review of his work he expresses himself rather cautiously in regard to the conclusions to which Osborn points, saying, "While admitting the paucity if not the total lack of direct evidence in this field I still lean strongly towards the view that the process of natural selection must be supplemented by adaptive responses of a more direct nature."

My own work, however, permits, I think, of taking a definite stand towards both problems, mentioned in Osborn's sentence which I quoted before, namely, the problem whether the formation of subspecies is the beginning of speciation and whether unknown actions of the environment are responsible for the adaptational features of geographic variation. Regarding the second point, I could prove that certain characters of a more physiological order show within the geographic range of the species a gradient of different heritable conditions which are perfectly parallel to a gradient of certain climatic conditions. For two of these characters, namely, the length of time of hibernation, the so-called diapause and the rate of larval growth, it could be shown in detail that the definite hereditary type found in definite areas constitutes an adaptation of the life-cycle of the animal to the seasonal cycle of nature. To mention only one example, which is typical for all similar cases: In a region with strong winter and short summer the hibernating individuals would be wiped out if they hatched too early; on the other side, the race would be wiped out if they hatched so late that the short summer would not give them enough time to finish their life-cycle. Correspondingly, the genetic constitution of the races inhabiting such a region is such that a certain sum of heat makes the individual hatch within a short time, whereas races inhabiting warmer areas with mild winter require a much larger sum of heat for the same purpose, also on a hereditary basis. And of course all imaginable intermediate conditions are also found in their proper area.

Here, then, we have a series of typical adaptations

to the conditions of a series of typically different environments, and these adaptations are caused by different constitutions in regard to Mendelian genes. Changes in the genetic make-up concerning individual genes are known thus far only to occur in the form of mutations, and no geneticist will doubt therefore that also in this case the different genetic constitutions of the races, those with and those without adaptational value, are the result of mutations and their proper recombinations which once must have taken place in the same manner as mutations observed in the laboratory. But how about the adaptational side, in our case the close parallel between the gene-controlled details of the life-cycle which we just mentioned and those of the seasonal cycle in different regions? If I am not mistaken, Davenport and Cuénot were the first to pronounce the principle of preadaptation, which to most, if not all geneticists, seems to furnish the only workable idea in cases like the one here discussed. Preadaptation means that adaptations are not originated in the surroundings in which they are found and also not caused by whatever action of these surroundings; moreover, adaptive characters appear as chance mutations, without any relation to their future adaptational value, as preadaptations. But these changes allow the organism to migrate into new surroundings, into which it will fit on the basis of its preadaptations. Applied to our case, it would mean that among the population in the original environment mutations were found which produced different conditions in regard to adaptational characters, in our example, mutations which prolong or shorten the inherited length of the hibernation period. Such mutated forms were preadapted to another environment. Brought by chance into another environment with a correspondingly different seasonal cycle, they were able to establish themselves. It is needless to say, then, that we must regard such preadaptational mutations as a prerequisite for the spreading of a species into new areas with different conditions, which would be inaccessible to the original form, and therefore also for the formation of geographic races or subspecies; and further that it will be the physiological characters, not the visible traits, which will be of primary importance in this case. In my material, *Lymantria*, as a matter of fact the diversity of physiological characters is considerably greater within the Rassenkreis than the diversity of forms which the taxonomist could recognize.

May I mention finally two facts which show the principle at work in our material. Every American knows that the few caterpillars of the gipsy-moth which were blown out of Monsieur Trouvelot's window two generations ago established themselves only two

well in Massachusetts. In the light of our work their hereditary life-cycle must have been well preadapted to the seasonal cycle in Massachusetts. The same moth has been introduced into England any number of times, but never was established, in my opinion only for lack of preadaptation to the seasonal cycle. The second fact is the following: Some years ago, I had succeeded in producing mutations in *Drosophila* by the action of high temperature. The Japanese geneticist, Y. Tanaka, informed me then that he succeeded in producing mutations in the silkworm by a similar method applied at a definite stage. I then occasionally treated the gipsy-moth in a similar fashion. One mutation, which was produced, made the young caterpillars hatch without hibernation. Within the present range of distribution of the moth, such a mutation, if occurring in nature, would be absolutely lethal, because in a moderate climate there would be no possibility of finishing a second generation before winter sets in. But introduced into a tropical climate, the same mutation might permit the otherwise unlikely establishment of the form. I do not doubt, then, that the adaptational side of the facts of geographic variation is to be explained on ordinary genetic grounds, namely, chance mutation of preadaptational nature within a population and subsequent migration into and survival in another suitable area. I may add finally that our material is not the only example, but that Brown has since found a parallel case in *Daphnids* and that also Turesson's work on ecospecies in plants fits perfectly into these lines.

Let us turn now to the other problem stated above and answered in the affirmative by Osborn and probably by most taxonomists: Is the formation of geographic subspecies the beginning of speciation? My own work was started with the idea of proving that it was. As I have already stated at last year's International Congress of Genetics, the results of the analysis led me to the conclusion that it was not. The different subspecies in the different regions occupied by the species are genetically different in many characters. Most of these are found to form quantitative gradients which run parallel to definite features of the climatic conditions. But the series of local changes in regard to one character is not exactly paralleled by those of other characters, so that in a given area one hereditary and differential character might be found over the whole area, another be subdivided into three types and another into more types. But I was unable to find one or a combination of subspecific characters which could be regarded as leading out of the limits of the species or towards another one.

There are found within the same region two other species of the same genus which show practically the same life-cycle and which must be adapted to the same

general features of the region. But they are different in practically every detail of their form, structure, larva and even their type of genetic variation. Of course their differences might be also adaptational in a certain sense. But here is the great difference: The different adaptational characters of the subspecies are of a quantitative nature, and show a plus-minus character. For example, we find a longer diapause in warmer and a shorter in colder regions, similarly different rates of development, different sizes, degrees of pigmentation, etc. The adaptation to local conditions then takes place by genetic shifts of a quantitative nature within the typical characters of the species and, as I may now add, running in the same directions as the non-heritable reactions to the environment. The different species, however, may solve one and the same adaptational problem by entirely different methods. For example, the species *Lymantria dispar*, the gipsy-moth, lays her eggs in the shade on wooden or stony surfaces and covers them with a sponge-like mass of hair, the problem being to ensure proper conditions for hibernation, especially regarding moisture. The nearly related species, *L. monacha*, pastes her eggs without covering into clefts of the bark of trees, and another species, *L. mathura*, still in the same area, lays below the bark and within a cement-like mass. Of course, within the different genetic systems represented by related species, parallel types of genetic variation, subspeciation, may be found, as is well known. For example, many species of rodents may form pale desert forms, and many species of birds form subspecies with brighter colors in warmer climates. But in other cases even the trend of genetic variation might be different: *Lymantria monacha* tends towards formation of melanic forms; *L. dispar* does not. These two species are able to spread all over the moderate regions by proper adaptive changes, but not into the tropics, the nearly related species *L. mathura*, however, inhabiting certain regions together with the former, spreads into the tropics but not into cold regions.

I am perfectly aware of the dangers of generalizing from one case, even the best known one. I know also the objections to such conclusions, for example: There are Rassenkreise, the most distant members of which might be so different that in case of isolation they might become the starting point for quite new developments towards another species. Looking closely at the facts concerning the typical differences within a Rassenkreis, I can not see why the isolation of two members of a Rassenkreis could give better chances for new developments than the isolation of individuals within a subspecies: The changes necessary for the formation of a new species are so large that the relatively small differences of the subspecies as a starting point would hardly count. And I can not help

confessing that after trying to get acquainted with the taxonomist's material, the skeptical standpoint derived from my own genetic analysis could not be shaken. There is in my opinion no reliable fact known which would force us to assume that geographic variation or formation of subspecies has anything to do with speciation; the results of genetical analysis and of sober evaluation of the other facts are positively in contradiction to such an assumption.

We just mentioned the fact that different species—and also as a matter of fact members of different families—may show a trend towards formation of comparable mutations and parallel series of subspecies, which are, after all, combinations of mutations strained through the sieve of fitness to environment. It is known that especially Vavilov has made such facts the basis of evolutionary considerations. But we also mentioned that nearly related species might show different trends of genetic variation. And this leads us to a point which, I believe, will be considered of paramount importance in future discussions of evolution. The transformation of one species into another is possible only if permanent changes in the genetic make-up occur, and if the changed forms stand the test of selection. Both these points have long been in the foreground of evolutionary discussion. But there is a third point, often neglected, which lies, I think, at the basis of the whole problem, namely, the nature of the developmental system of the organism which is to undergo evolutionary change. The appearance of a genetic form, whether we call it a species or a genus, which is to be considerably different from the ancestral forms, requires that a considerable number of developmental processes between egg and adult have to be changed, in order to lead to a different organization. Development, however, within a species is, we know, considerably one-tracked. The individual developmental processes are so carefully interwoven and arranged so orderly in time and space that the typical result is only possible if the whole process of development is in any single case set in motion and carried out upon the same material basis, the same substratum and under the same control by the germ plasm or the genes. From this it follows that changes in this developmental system leading to new stable forms are only possible as far as they do not destroy or interfere with the orderly progress of developmental processes. Of course, everybody knows that this is the reason why most mutations are lethal. But not everybody keeps in mind that here also is touched one of the basic points of the problem of evolution. The nature and the working of the developmental processes of the individual then should, if known, permit us to form certain notions regarding the possibilities of evolutionary changes.

There are, as far as I can see, two general notions in regard to the causal understanding of individual development which are of importance for the problem under discussion. One is the notion which I have tried to develop from experimental evidence that the action of the genes in controlling development is to be understood as working through the control of reactions of definite velocities, properly in tune with each other and thus guaranteeing the same event always to occur at the same time and at the same place, as worked out in detail in my physiological theory of heredity. The second notion is that derived from the results of experimental embryology. It says that two types of differentiation are closely interwoven in the process of development, namely, independent and dependent differentiation. Independent differentiation means that a once started process of differentiation takes place within an organ or part of the embryo, even if completely isolated from the rest; dependent differentiation, however, requires the presence and influence of other parts of the embryo for orderly differentiation. If, for example, the group of cells which is to be regarded as the primordium of an eye in the embryo of a vertebrate, is removed from its proper place, it will nevertheless be able to develop into an eye. If, however, the part of the skin of the head which is to form the lens of the eye is isolated, no lens is formed because the presence of the eye is necessary for the determination of a lens. Such are the two general notions, which together describe fairly well the essentials of gene-controlled development, namely, the notion which considers development as an orderly interwoven series of developmental reactions of definite velocities, properly in tune with each other, and the notion of dependent and independent differentiation. Both together will allow us to discuss some of the possibilities of evolutionary change as viewed from the standpoint of stable, orderly development.

Let us begin with an experimental fact. It has been known for a long time that it is possible to change the appearance of certain butterflies by proper experimental procedure within a sensitive period of development so that they can not be distinguished from heritable geographic subspecies found in nature in other regions. If, for example, the young pupa of the Central-European swallowtail is treated with extreme temperatures, some individuals will hatch which can not be distinguished from the typical forms inhabiting Palestine. Of course the characteristic features are not heritable in the former case, but strictly heritable in the latter. These and similar facts have since been extended in many ways, also to cases of ordinary gene mutations. I was, for example, able to produce in similar experi-

ments with *Drosophila* the non-heritable likeness of many well-known mutations. I do not doubt either that it would be possible to perform the same experiment in regard to any known mutations, if the proper method would be found. Speaking generally, this would mean that the more frequently occurring genetic changes, called mutations, are such as change certain developmental processes in a direction which lies within the ordinary range of changes which might occur within the developmental system under purely environmental influences. An explanation is very simple on the basis of the assumption that in the developmental processes in question reaction-velocities are involved; the external influences in question change the rate of some reaction or system of reactions underlying the differentiation of the character in question and the mutation which produces the same phenotypic effect is a change in a gene, which controls the same differentiating reaction, with the effect of a corresponding change of the speed of the reaction. It is perfectly clear, then, that within similar developmental systems, represented by taxonomically related forms, the same types of mutational changes, parallel mutations, will have the greater chance of not being lethal, because in such a system of exactly tuned and interwoven reactions, only few changes of the rate of individual processes will be possible which do not interfere with the others. And there is another consequence: if there are only a few avenues free for the action of mutational changes without knocking out of order the whole properly balanced system of reactions, the probability is exceedingly high that repeated mutations will go in the same direction, will be orthogenetic. Orthogenesis means that evolution, once started, proceeds further in exactly the same direction until sometimes extreme forms are evolved which lead to the ultimate extinction of the whole line. Paleontologists have found the most beautiful examples of this type, facts with which any theory of evolution has to reckon. Many theories have been advocated to explain such facts. We have pointed out a long time ago and still hold that orthogenesis is not the result of the action of selection or of a mystical trend, but a necessary consequence of the way in which the genes control orderly development—a way which makes only a few directions available to mutational changes, directions which if once started and not acted upon by counter-selection, will be continued. I shall not go into the purely genetic details of such a situation. But it might be mentioned that recently some of the younger generation of paleontologists (Beurlen, Schindewolf, Kaufmann) have taken up these views. This is indeed very gratifying, because the problem of orthogenesis has always been a stumbling block to an understanding between geneticists and paleontologists.

At this point, we have to think of the second notion, mentioned before, regarding the general control of embryonic differentiation, namely, dependent and independent differentiation. It is obvious that processes of dependent development are so closely linked with the whole of normal development that mutational changes within them can hardly lead to a normal organism. It is therefore to be expected that successful mutations of eventual evolutionary value act upon such developmental processes which themselves are not inductive of further important steps. This means that viable mutations will mostly be concerned in the animal kingdom with end-processes of embryonic differentiation, affecting the organism only after the characteristics of the species have been laid down.

But how about the possibility of occasional successful mutational changes acting upon earlier developmental processes? Would such a change, if possible at all without breaking up the whole system of the orderly sequence of development, not at once have the consequence of changing the whole organization and bridging with one step the gap between taxonomically widely different forms? Let us for a moment dwell upon such an idea, which I pointed out a long time ago as a logical consequence of my views on gene-controlled development and which has repeatedly cropped up since in evolutionary literature (*e.g.*, De Beer, Haldane, Huxley). Again, the most probable mutational change with a chance to lead to a normal organism is a change in the typical rate of certain developmental processes. Of course, in most cases such a shift of a partial process would lead to the production of monstrosities and, as a matter of fact, Stockard has always advocated such a cause for many monstrosities. But we must not forget that what appears to-day as a monster will be to-morrow the origin of a line of special adaptations. The dachshund and the bulldog are monsters. But the first reptiles with rudimentary legs or fish species with bulldog-heads were also monsters. Correspondingly, we certainly know of many cases of mutational shifts of the rate of certain developmental processes leading to non-viable results, for example, caterpillars with pupal antennae, larvae of beetles with wings and similar cases of so-called pro- and opisthotely. But I can not see any objection to the belief that occasionally, though extremely rarely, such a mutation may act on one of the few open avenues of differentiation and actually start a new evolutionary line. Let us assume a mutational change in rate of differentiation of the limb-bud of a vertebrate, to take up the example just mentioned. The consequent rudimentation of the organ would probably not interfere with orderly development of the organism. Here, then, an avenue would be open to considerable

evolutionary change with a single basic step, provided that the new form could stand the test of selection, and that a proper environmental niche could be found to which the newly formed monstrosity would be preadapted and where, once occupied, other mutations might improve the new type. And in addition, the possibility for an orthogenetic line of limb-rudimentation would be a further consequence in accordance with what we have heard before. Of course, these are speculations, which we can not help but enjoy occasionally as long as unfortunately there is no way visible of attacking such problems with the methods of genetics. But meanwhile some important insight might already be gathered from purely morphological work, as that of Sewertzoff, or experimental work of the type of Twitty's work on rudimentary eyes.

At the best, such viable mutations concerning rates of earlier developmental processes must be rare, even when processes are involved such as the differentiation of appendages which are not so closely interwoven with the whole of development. Still lower is the chance if we try to imagine changes in differentiation which are of consequence for the whole of development. Let our imagination run wild for a moment and let us consider the possible event of three more and more violent and therefore less and less probable changes of the type under consideration, produced by a viable mutation acting upon earlier embryonic differentiation by changing relative rates of development. D'Arcy Thompson has shown that extremely different forms of organs or of whole organisms may be geometrically transformed into each other by a Cartesian transformation of the system of coordinates. Translated into phylogenetic language, this would mean that immense evolutionary effects could be brought about by changing the differential growth rates of the whole body or organ at an early point in development, with all the necessary secondary effects of such a change. I could imagine, and I have actually pointed out, that a single mutation involving the rate of one of the important reactions connected with growth, acting on the principle underlying Thompson's transformations, could start a perfectly new evolutionary line, leading at once far away from the original form and being able to be completed by orthogenetic development within the once blasted new avenue. Or another example: There are innumerable cases known where no intermediate forms between two extremely different ones are imaginable. Take, for example, the Pleuronectid fishes, the flounders and their kin, lying flat on one side, the eyes being translocated during embryonic development to the other side with all the following asymmetries of skull, fins, muscles. Cuénot expressed his conviction a long

time ago that no slow accumulation of variations and selections is needed to explain the origin of such forms. There exist flat symmetrical fishes with the habit of resting lying flat on one side. Given the proper arrangement of the eye muscles and the inter-orbital septum of the skull, a single step was only necessary to start the migration of the eye, all the rest of the transformations being necessary consequences of the first step. I can not help agreeing with Cuénot and adding that at the proper moment in the evolutionary line a single mutation in regard to the rate of certain embryological processes of the type which ordinarily produce a monster, may have given birth to a monstrous new family with all its essential traits and preadapted to certain modes of living. Of course the further differentiation, the slow evolutionary working out of the details, would be brought about by new mutations of the different types, including as well other large steps, as accumulations of small mutations under the influence of selection.

A third example, which I have repeatedly used to explain the general idea, appears still more fantastic. Let us consider one of the famous lines of transformation which the comparative anatomy of vertebrates has brought to light, for example, the series of transformations of the visceral arches. I believe that these facts constitute one of the most beautiful proofs of evolution; and in addition I believe that their analysis by the methods of comparative anatomy is one of the greatest achievements of biological thinking, though some biologists of to-day are inclined to prefer the most meaningless experiment to such a piece of masterful morphological analysis. In the case of the visceral skeleton we see, for example, that the so-called hyomandibular bone of fishes loses its function as connective element between jaws and skull, and is transformed into an auditory ossicle situated within the skull and playing an important rôle in the transmission of sound, a transformation which takes place simultaneously with the appearance of the tympanical membrane as adaptation to terrestrial life. In this transformation two major steps are observed: First, the formation of a new connection between skull and jaw, thus excluding the hyomandibular bone from its former function; second, the appearance of the tympanical membrane in this region and the inclusion of the hyomandibular bone into the ear cavity, with the change of its function to that of an auditory ossicle. The first step is found in the Crossopterygian fishes, the second in Amphibia. In both cases a slow transformation by accumulation of advantageous mutations is hardly imaginable. There are no steps possible between a tympanical membrane and none and also no steps between two

types of articulation of the jaw with the skull. But I could not find much difficulty in the idea that the decisive step was taken by a single mutation affecting the relative rate of differentiation of the cranial end of the hyoid arch from which springs the hyomandibular bone, with the effect of forcing these parts, left behind in development, into new surroundings and connections, where future developments could make use of them for quite different purposes. It would certainly be of no use, and sheer speculation, to try to work out such an idea in detail. But I think that we can get hardly around the principle underlying it. Of course, there is no way visible to attack such a problem by the methods of genetical research. But I am not so sure that this means that it can not be attacked at all.

At the beginning of this lecture I said that my mind, like that of many geneticists, is oscillating between skepticism and optimism with regard to the views on the means of evolution as derived from genetical work. I have now presented to you examples of both states of mind: First, a bit of skepticism with regard to the rôle which the formation of geographic races or subspecies may have played in evolution; and then a bit of optimism in trying to show that the physiological system underlying orderly development, on the basis of the genetic constitution, allows some of the larger steps in evolution to be understood as sudden changes by single mutations concerning the rate of certain embryological processes. But whoever tries to formulate views on the means of evolution on the basis of the actual knowledge of facts must be aware that any day new facts might come to light which could force our ideas into quite different channels. Therefore I wish to return at the end of this lecture again to the results of actual experimentation and to draw your attention to some new lines of experiment which perhaps will finally influence our general conceptions considerably.

A number of years ago I found, as already mentioned, that it is possible to produce gene mutations by the action of extreme temperatures of almost lethal dose. Unfortunately, there is still an unknown element in the technique of these experiments which makes success dependent upon some conditions which have not been isolated as yet. Progress in this line of research is therefore slow. One of the most startling results of this work was that in a series of experiments a few mutations were always produced again. Jollos, who continued this work, had similar results, but in his experiments other mutations were preponderant and also appeared over again. I then repeated the experiments and in successful cultures had now the same mutations which appeared also in Jollos' cultures. Thus it seems that there is a rela-

tion between stimulus, maybe also material, and the type of genetic response. There was another interesting result. I have mentioned already that in such experiments quite a number of phenotypic changes are produced which resemble well-known mutations, but are of the nature of non-heritable modifications. In a few instances, cases were found where the treated animals themselves showed such a visible change, namely, dark body color, and where the offspring of the same animals showed the same phenotype as mutation. The explanation which had to be given to such a case of so-called parallel induction was that there was simply a chance-overlapping of two independent phenomena, namely, the production of a modification and of a mutation of the same phenotype; this would be made possible by the aforementioned assumption that in both cases the same developmental process was changed either by environmental action or by genic action.

But there were still other strange facts. I had observed that the typical non-heritable changes which resembled heritable mutations in appearance, and which always were found in the flies which had been treated with heat during definite larval stages, were different, if the details of treatment were changed. For example, with one type of treatment, a certain peculiarity of the wing-shape was produced; with another type of treatment the majority of changed individuals presented a very different type of wing-form. In recent experiments, Jollos, who had had the same experience, could add some most interesting facts. In the lines with ordinary treatment the most frequent mutations were those of body color, called sooty, and of eye color, called eosin. If the usual treatment was replaced by one with dry heat, the non-heritable variations which appeared in the treated animals were of a different type than usual. Predominant were flies with extended wings, with curly wings, with asymmetrically shortened wings and with scalpelliform wings. Jollos continued treating the normal offspring of these lines with the same method, and during the following generations a number of mutations appeared, some repeatedly; and among these were the mutations, the phenotype of which is identical with the forementioned non-heritable variations produced in the same line, namely, extended, curly, scalpelloid and asymmetrically shortened wings. Of course, this has nothing to do with an inheritance of acquired characters; the mutations had appeared among the offspring of normal individuals. There are now altogether seven cases in which a mutation has been produced in the same lines in which exactly the same phenotype occurs frequently as a non-heritable modification as a consequence of the same

treatment. Among these seven cases, one of which was found by myself and the others by Jollos, is one mutation which before was observed only once in the whole *Drosophila* work and two which had never been observed.

These certainly are interesting facts, which might lead to strange consequences. I personally am willing to wait for further results before drawing conclusions. Jollos, who has not yet published the results which I quoted, permits me to mention that he is inclined to derive the following interpretation: The genes produce within the protoplasm active stuffs which are of the same constitution as the genes themselves. Both will react in the same way upon external conditions, but those within the protoplasm easier than those protected within the chromosomes. Such a view, of course, would lead to many interesting consequences. We shall, however, dismiss the subject with the mention of the actual facts, which one day may be of great importance not only for problems of special genetics but also for discussions on evolution.

The title of this lecture was: "Some Aspects of Evolution." But as I said at the beginning, it was not meant that the idea of evolution itself, which all biologists consider a historic fact, should be under discussion, but some of the ways and means by which nature makes the transformation of species possible. The three aspects which I chose for representation were, first, an aspect where I had to express skepticism in regard to well-established beliefs. I tried to show on the basis of large experimental evidence that the formation of subspecies or geographic races is not a step towards the formation of species but

only a method to allow the spreading of a species to different environments by forming preadaptational mutations and combinations of such, which, however, always remain within the confines of the species. The second aspect which I discussed was one where I felt again optimistic. I tried to emphasize the importance of the methods of normal embryonic development for an understanding of possible evolutionary changes. I tried to show that a directed orthogenetic evolution is a necessary consequence of the embryonic system which allows only certain avenues for transformation. I further emphasized the importance of rare but extremely consequential mutations affecting rates of decisive embryonic processes which might give rise to what one might term hopeful monsters, monsters which would start a new evolutionary line if fitting into some empty environmental niche. Finally, I discussed a third aspect of the problem, this time under the slogan of watchful waiting, namely, new lines of genetic research concerning the problem of mutation and therefore also of evolution. With these discussions we touched certainly only a small fraction of the manifold problems of evolution. But if we would try to visualize all the contributions which the science of genetics has recently made in this direction, we might be entitled to say that our insight into one of the most complex biological problems is constantly increasing. Progress of science follows of course a slowly ascending, wavy curve, with always recurring valleys. But viewed from some distance, the waves disappear and only the upward trend remains visible. Such is also the case with our knowledge of the methods and means of evolution.

OBITUARY

MEMORIALS

CEREMONIES commemorating the one hundredth anniversary of the birth of Dr. Carlos J. Finlay, who first advanced the theory that mosquitoes were carriers of yellow fever, were held at the Cuban Embassy on December 3. The ceremonies were due to the initiative of the Washington chapter of the Pan-American Medical Society, with Dr. Manuel Marquez Sterling, diplomatic envoy of the Cuban Government, acting as host. The program included addresses by Dr. Sterling, Senor Don Luis M. de Iruju, Spanish chargé d'affaires; Colonel Roger Brooke, of the Army Medical Department; Dr. L. O. Howard, Brigadier General J. R. Kean and Dr. Victor Alfaro.

MRS. ERNEST HOWE, of Litchfield, Conn., widow of Ernest Howe, who died last December, has given to Yale University \$10,000 for the establishment of the Ernest Howe Memorial Fund. The income of the

fund will be used to promote the study of the geological sciences at Yale. Mr. Howe, who graduated from Yale College in 1898, was editor of the *American Journal of Science* from 1926 until his death. In addition to his research work, he was geologist of the Isthmian Canal Commission, was invited by the Mexican Government to reorganize its geological survey and was geologist on the scientific expedition to Brazil headed by Dr. Hamilton Rice under the auspices of the Royal Geographic Society of London. He was elected to a term in the Connecticut Legislature in 1920 and in 1924 was elected to the Connecticut Senate.

THE *Journal* of the American Medical Association reports that the one hundredth anniversary of the publication of William Beaumont's "Experiments and Observations on the Gastric Juice and the Physiology of Digestion" was celebrated by the St. Louis Medical