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THE TREND OF MORPHOLOGY[1]

THE trend of morphological investigation has seemed to me a particularly appropriate topic for consideration before the American Association of Anatomists on this occasion. Others might suppose that since all of us are morphologists we are naturally familiar with this trend and such a discussion is out of place or useless. Yet are we as workers in a science always conscious of its trend, or is the trend the same in the minds of any number of us? It may be that each sees the trend from the view-point of his own endeavor and any one might have difficulty in convincing his colleagues that he is looking straight forward rather than sidewise or possibly even backwards. The exact direction of progress is somewhat problematical and attempting to follow it becomes an experimental venture, since the speaker is forced to employ his own personal compass and takes the chance of being alone or in a company of questionable size when the end of the survey is reached. In spite of the risks involved, I shall attempt to trace an impartial outline of the growth of morphology with an analysis of its sudden modifications at the beginning of this century and the possible effects of these on its immediate problems.

The very early history of the subject has no place in such an outline, and a convenient point for starting is with the introduction of the definite term *morphology*. It is strangely interesting that this word was first used by one of the most romantic poets of history, who at the same time chanced to be an eminent morphologist of the early nineteenth century. Goethe, in 1817, employed the word to indicate unity of structure in place of the more awkward term *metamorphosis* which had been applied in a similar sense by the great naturalist Linnaeus. Goethe's instinctive biological ideas frequently occur even in his poetry and drama—in the poet's great masterpiece Mephistopheles remarks to Faust the oft-quoted morphologic truth, "Blut ist ein ganz besonderer Saft!" All hematologists are still unwilling to disavow it.

The investigation of living mechanisms considered as the structural side of biology has followed in its history something of a parallelism with the two other great natural sciences—physics and chemistry.

[1] Address of the president of the American Association of Anatomists, University of Rochester, New York, March 27, 1929.

Throughout their early periods the three sciences were almost entirely concerned with the study of crude masses of stuff. It was not until near the beginning of the nineteenth century that rapid advance was made in approaching the true composition of physical matter and the arrangements of the finer parts in the living organism. The old phlogistic doctrine in chemistry was overthrown by Lavoisier only during the final quarter of the eighteenth century. And it was during the last century that matter displayed to the chemist much of the nature of its atoms and molecules through methods of accurate quantitative analysis and measurement, and that physics advanced so rapidly in its mastery of the energies of heat and electricity. Also during this period, and long after the invention of the microscope, living animal and plant bodies were seen to be composed of their organizational units, the cells, and many of the important intracellular elements were discovered and deeply considered by morphologists.

Again the parallelism persists in that near the beginning of the present century discoveries were made which completely revolutionized the future development of the three natural sciences! As Professor Millikan[2] has strikingly expressed it for physics:

> . . . in 1893 so sure were we of the physical foundations of our world . . . that it was then being frequently said, often by the ablest of physicists, that it was probable that all the great discoveries in physics had already been made and that future progress was likely to arise only by increasing the refinement of our measurements. Then came, only two years thereafter, the capital discovery of X-rays, an entirely new phenomenon, having no relation whatever to refinements of measurement. And two years later came radioactivity, which has now completely exploded the notion of the eternal character of the atom and revealed a world in which many if not all of the so-called elements are continually undergoing change. . . . And then three years later came the beginnings of the quantum theory, which has shown us unmistakably (so it appears) that in the domain in which electrons live even Newton's laws no longer hold.

By strange coincidence, at just about the same time the laws of heredity, discovered thirty-five years before by Mendel but completely unappreciated by the biological workers of that day, were rediscovered when the state of morphological knowledge was so exactly ripe for a general comprehension of these laws that a sudden impetus shot through the entire realm of biology, revitalizing its twentieth century progress.

These great discoveries near the close of the century have advanced the quest for the ultimate nature of structure to a study of the interior of the atom, electronic arrangement, and of the interior of the cell nucleus, the arrangement of the chromosome and the gene. Thus all qualitative differences have come closely down to an ultimate problem of arrangement! Had the exploitation craze of to-day sufficiently impressed this association we might proclaim—universal morphology!

Here general comparisons must finish and we proceed with the discussion of the limited subject with which we are more suitably qualified to deal.

In order to sufficiently evaluate the importance of the earlier contributions as a foundation for the twentieth century renaissance in morphology we may consider very briefly the morphological interests of the nineteenth century.

During the early part of the century a morphological foundation for a clear exposition of the theory of evolution was being carefully laid. The morphologists of that time fully recognized the relationships of organisms on the basis of their common structures, and they arranged animals and plants in accord with the various degrees of similarity which clearly divided them into more nearly and more distantly related groups. Homologous systems and organs were particularly recognized throughout the vertebrate kingdom, and slightly graded differences in these structures were found among closely similar and apparently related species. Many morphologists were definitely convinced that organic evolution had taken place and that this phenomenon accounted for these structural homologies.

Cuvier may be called the most conspicuous comparative anatomist of the early years of the century, although the philosophic side of anatomy did not strongly appeal to him. His influence and discussions, however, stimulated study which was carried on in France by a list of able anatomists—de Quatrefages, A. Milne-Edwards and Lacaze-Duthiers; in Germany by Bojanus, von Siebold, J. F. Meckel, Johannas Müller and others; while in England Sir Richard Owen was the leading exponent of this school.

Somewhat contrasted with these investigators and probably, from a modern standpoint, in advance of them was a more transcendental or philosophic school clearly led by Geoffroy St. Hilaire and conspicuously supported by Goethe and Oken. St. Hilaire's brilliant contributions, "Philosophie Anatomique," 1818–1823, present an array of surprisingly analytical deductions among which are contained fundamental conceptions of structure and important doctrines of development. The unity of organic composition and evolution were appreciated in complete harmony with the ideas shortly before advocated by Goethe. The theory of analogies emphasized the fact that the same parts differing in structural degree occur in all ani-

[2] "The Practical Value of Pure Science," SCIENCE, 59: 9. January, 1924.

mals. Yet the most remarkable conception was St. Hilaire's "principe du balancement des organs" upon which he founded the study of abnormal development or teratology, and claimed in a clearly modern sense that the high development of one organ is associated with a suppression or a diminution in the development of another. This conception anticipated by almost two generations Roux's ideas of "der Kampf der Teile," or the struggle of the parts in the developing organism. Some of the most recent findings in experimental embryology add convincing demonstration of the truth of the "principe du balancement des organs" as expounded more than a century ago. The idea is, therefore, old, but the experimental proof of its truth is so recent that some are at times inclined to feel that in demonstrating the fact they actually originate the idea—but not so. Long ago was visioned

> The nations' airy navies grappling in the central blue,

but the actual demonstration was painfully recent. The demonstration, after all, is the vital thing in science.

Any one viewing the history of biology during the early part of the past century will be impressed by the paramount rôle which morphology played in bringing the human mind to realize that organic evolution had taken place. In fact, it is difficult to conceive how from any other than the morphologic standpoint evolution could have been comprehended. This is recognized without any intention of reflecting on the physiological phase of the problem. It is perfectly fair to point out the peculiar prominence of one division of biological study in any particular conception. Morphology and physiology are not competitive or antagonistic fields or points of view, but structure and function are indelibly correlated and mutually dependent parts of one whole, if not actually the same thing! The function of an automobile depends not only upon the structure of its parts but their arrangement as well, and no one will deny that the functioning of the machine alters its structures until their arrangement ceases to be an automobile. The performance of a mechanism reacts on its structure so that the modified structure gives new function and the two phases therefore move together.

The vast sum of knowledge accumulated by comparative morphology before the latter quarter of the nineteenth century had largely been amassed on the simple basis of descriptive observation. There had been scarcely an intimation of effort to analyze experimentally or test the meaning of structures. Morphological descriptions had become more and more exact and minute in their detail, and morphometry had been developed to a considerable degree. Histology had been founded by Koelliker and cellular pathology by Virchow, whose aphorism *omnis cellula e cellula* was vigorously advocated as a fundamental law. At this stage, during the last quarter of the century, a most fortunate innovation occurred for the science of morphology with the introduction of the experimental method. The movement originated and first developed in Germany, but was soon introduced into the biological laboratories of this country. The names of Roux, Oscar and Richard Hertwig, Driesch, Boveri and others are among the pioneers in this method of attack which many would claim actually started morphology on a strictly scientific basis.

It must at once be recognized that we are referring to the introduction of the experimental method particularly into morphology and embryology rather than into the broad subject of biology. No one forgets that many of Darwin's painstaking and long-carried-out studies were partly experimental, and he, of course, always displayed a penetrating appreciation of nature's own experiments as well as of that great experiment to which so many forms, including man himself, have been subjected—domestication. Other accidental and more or less disconnected experiments are recorded in the history of biology for centuries back, but a systematic experimental morphology and the analytical study of the development and formation of structures was actually begun by Wilhelm Roux, the anatomist of Halle, as truly as by any one person. And this experimental attack was quickly adopted by many of his countrymen and, next in order, by American workers. There were early studies of polarity, of the predetermination of the embryonic axis, of germinal localization or promorphology in the unfertilized egg through efforts to fragment the egg, of potencies in the segmenting egg through the separation of blastomeres, the destruction of certain regions of the egg, the inversion of the egg and many other more or less mechanical performances.

These early experimental studies brought the problem of morphology closely down to the potentialities of the embryonic cells as the units of structure and revived on a modern basis what one may call the "cell theory." Certain things were appreciated, however, such as multinuclear cells—syncytia, etc., which caused some investigators to question the validity or the universality at least of the cell doctrine.

Looking back on these discussions of the inadequacy of the cell theory we realize that from our present standpoint the actual boundaries of the cell and other contra arguments are not necessarily of great import, and from a pragmatic point of view biological reasoning is greatly facilitated by an appreciation of the cell not as an ultimate simple unit but as the ultimate biological organization.

One of the most fascinating and fundamental chapters in morphology is that concerted study of the nuclear structures of the cell during the last two decades of the nineteenth century. We must here give attention to the significance of some of these studies, since through them the foundation was laid both for an analysis of the phenomenon of inheritance and an understanding of the structural behavior within the cell. The controversial cell theory becomes lost in the vigorous consideration of the individuality of the chromosomes within the nucleus. These bodies and something of their behavior during cellular reproduction had for some time been known before they were christened in 1888 by the eminent anatomist Waldeyer as "chromosomes." Five years earlier W. Roux in his study "Über die Bedeutung der Kernteilungsfiguren" had supposed that the formation of the chromosomes from long threads brought about an alignment in linear series of different materials or "qualities"! Then by longitudinal splitting of the chromosomes as an early step in nuclear division all the "qualities" are equally divided and passed to the two daughter nuclei. This interpretation by Roux is astounding in minute accuracy of conception, and actually in the light of our knowledge to-day it is equally as remarkable as Weismann's prediction of a reduction of the chromosome number during the maturation divisions.

It had become recognized through many studies that the chromosome number was constant for a given species, and Weismann in 1887 predicted on theoretical grounds that in order that the number might remain constant through generations there must be a place somewhere during the maturation of the germ cells at which the chromosome number is reduced to half and in bisexual reproduction the original number is again restored at fertilization by the union of the egg and sperm. Boveri in 1888 advanced a somewhat similar conception. The actual phenomenon of reduction was first observed three years later by Henking for the insect Pyrrhocoris, soon after for other forms by Häcker, vom Rath and others, but in particularly satisfactory detail by Rückert in 1894 for the copepod, Cyclops.

These studies of the reduction division gave emphasis to the importance of the rôle of the chromosomes and strengthened the idea of their individuality as cellular structures. The modern theory of the individuality of the chromosomes had already been promulgated in 1885 by the anatomist Karl Rabl. However, we recognize this theory as having been successfully championed by Boveri with a series of splendid studies extending through almost his entire scientific life.

The idea of the individuality of the chromosomes was actively opposed on the basis of the occurrence of amitosis before this method of division had been very fully understood. Science advances through a struggle with opposition—but it remains an open question whether the oppositionists actually aid in the advance. Much effort is often wasted in vain attempts to convince contrary minds of the actual direction from which the light comes.

We may now say that during the past thirty years such a formidable array of evidence has accumulated in support of chromosomal individuality that no reputable cytologist longer fails to accept it. Not only is this true but the individuality of the chromosome has been further advanced to the "theory of the gene." And this theory has rapidly gained through the experimental analysis of linkage, crossing-over, non-disjunction and other morphological conditions through which the loci for many of the genes are now mapped in series along the chromosomes, in one animal form at least.

Much of the advance in our knowledge of finer morphological arrangements was contributed by anatomists of the European medical faculties—Flemming, O. Hertwig, Rabl, Roux, Rückert and many more, but in this country until very recently such studies have been confined almost entirely to the zoological laboratories of the universities—and this is somewhat of a reflection on our anatomical situation.

Just when the knowledge of cellular morphology had reached so advanced a position an apparently unrelated event occurred in biology—the rediscovery of Mendel's laws of heredity. One is justified in referring to this event as apparently unrelated to cellular morphology, since Bateson, himself one of the rediscoverers of Mendel's laws, was never quite able to fully appreciate the morphological background in analyzing heredity. These laws, which involve a sorting out or segregation of characters during inheritance, were, nevertheless, quickly linked with the behavior of the chromosomes in the maturation of the germ-cells and the fertilization of the egg.

The germ-cells, as we know, have when immature the diploid or double set of chromosomes, but in passing through the transformation into either spermatozoon or egg the chromosomes arrange themselves in pairs, and then a peculiar type of division takes place in which the chromosomes do not split as in ordinary cases but the members of each of the chromosomal pairs separate and a single chromosome goes into one of the daughter cells and its mate goes into the other. In the chromosomal pairs one member is derived originally from the mother and the other from the father, as Montgomery first suggested in 1901. He further emphasized the peculiar fact that although this side-by-side pairing of the chromosomes, synapsis, in the maturation of the germ-cells actually comes at the very end of development it is, nevertheless, the final and most minutely accurate step in fertilization. Each mature germ-cell receives only one or the other, either the paternal or the maternal, member of every chromosomal pair, and the total chromosome number in each cell is thus reduced to half. The behavior of the chromosomes, therefore, exactly parallels the behavior of the Mendelian characters since each unit derived from the father separates from the corresponding unit derived from the mother. The two factors of a pair are allelomorphs of each other. Their separation in the germ-cell is morphological segregation and on it depends the segregation of characters in the development of the offspring.

The first clear explanation of Mendelian phenomena on the basis of the behavior of the chromosomes was presented by a young student of zoology, W. S. Sutton, in 1902. Sutton recognized in the group of heteromorphic chromosomes of the grasshopper that each of these individual chromosomes was probably a qualitatively distinct thing carrying certain hereditary characters. He further thought that one chromosome might carry a number of characters. And he then pointed out the similarity between the processes of segregation in the reduction of the chromosomes and the inheritance of characters, and went further to explain that the chromosomal pairs segregate independently of one another just as two characters in Mendelian heredity may be transmitted independently. Two such characters were thus determined by factors located in different chromosomes. On the other hand all the factors carried by the same chromosome should tend to remain together, and the number of characters may be many times larger than the number of chromosomes. These ideas are now somewhat crude since we no longer have unit characters related to only a single factor, nevertheless, they were brilliantly conceived.

Very soon after Sutton's analysis, Bateson and Punnett in 1906 discovered the linkage of characters in inheritance but did not give a chromosomal explanation; however, Lock almost immediately called attention to the possible relation between linkage and the chromosomal hypothesis. Morgan and his associates have since discovered and arranged in a most definite way the four great groups of linked characters in Drosophila corresponding with the four chromosome-pairs in this animal.

During synapsis, the homologous chromosomes pair in such a manner that any factor or gene in one chromosome lies opposite the comparable factor or gene, its allelomorph, in the mate chromosome. In certain cases, Morgan, Sturtevant and Bridges have supposed that genes from one chromosome may cross-over or swap places with the comparable genes in the other chromosome of a pair, since certain characters in heredity actually cross-over, forming new linkage groups, as is shown by the expression of characters in the finished individual. Again there are cases in which the two chromosomes of a pair in synapsis fail to separate, and remaining together the entire pair passes into one of the mature gametes. This behavior during the reduction division is termed non-disjunction. When such a cell is fertilized a zygote is produced which carries an extra or additional chromosome and, correspondingly, it develops a confused complex of characters. This condition splendidly illustrates the influence of genetic constitution on ontogenetic development.

Through a systematic study of linkage and crossing-over, it has been possible to estimate the probable frequencies of crossing-over or the rearrangement of linkage groups. It is logically supposed that the closer together two genes lie in the linear arrangement of genes in the chromosome the less likely are they to be separated, and the further apart the more likely, when crossing-over does occur, and on the basis of cross-over frequency the loci of the genes in the linear chromosome have been carefully determined and the reliability of this map is constantly tested experimentally by the behavior of the characters in inheritance.

This modern study of genetics closely associated with a study of the physical structure of the cell and particularly with the chromosomal reactions has contributed a most astounding picture of ultimate morphology, and the story of the gene as presented by Morgan and his associates is comparable only to the quest of the atom and the electron.

In spite of the accuracy in location of the genes one must not form too simple an idea of the behavior of factors in inheritance. The complexity of the situation is due to the fact that many factors may affect the same character. As Morgan pointed out some years ago, "Red eye color in Drosophila, for example, must be due to a large number of factors, for as many as twenty-five mutations for eye color at different loci have already come to light." And further, "the factorial hypothesis disclaims any intention of making one unit character the sole product of one factor of the germ." In speaking of factors for eyes or for legs one must really mean differences in factor balance that produce effects only in the eye, the leg or other regions of the body.

We as anatomists should feel a peculiar satisfaction in that all these so beautifully delicate phenomena have been analyzed on a strictly morphological arrangement.

Morphology, then, has not only formed the fundamental basis for the establishment of the evolution and common relationship conceptions, but again cellular morphology lays the foundation on which modern genetics was begun and so brilliantly developed in this country. These facts must be appreciated in order to properly estimate the field in which we labor; yet not all morphologists fully realize their opportunities and responsibilities in these directions.

The changes thought of in association with embryonic development must now be considered in view of the necessity of relating these processes to the rôle of the genetic factors. To bring up our thread of the embryological side of morphology we find that the early mechanical experiments had before the end of the nineteenth century been supplemented by other experiments in which modifications in the chemical and physical environment of the embryo were employed.

The first experiments on modifications in the chemical environment seemed to give rise to particular types of structural defects as reactions to specific chemical treatments and, following the lead of Herbst with his "lithium embryo" of the sea urchin, it was a common fault to interpret these developmental reactions as specific responses to the chemical agent employed. The so-called lithium larva, for example, was later produced in several species of animal eggs. This larva showed a very peculiar deformity which was unknown in nature.

However, in treating vertebrate eggs with certain chemical substances, the speaker found in 1907 that well-known typical deformities could be consistently produced. This had important significance in advancing an understanding of structural anomalies and their origin. But in attempting to interpret the cause of a particular deformity the mistake was at first made of classing it as a specific response to the treatment used. During the following year, however, in experimenting with a number of different chemical substances or modifications of the environment I found that all these would produce the one definite developmental defect provided the eggs were treated during the same developmental stage. It was then realized, and recorded in 1909, that the defect was due to an anesthetic or slowing effect on the rate of development, and the following year it was shown with fuller results that the type of deformity was associated with the developmental stage of the egg at the time of the experimental treatment rather than with the specific nature of the treatment used. These results, in a way, though not until later appreciated, accounted for the constant repetition of the same type defect in the earlier experiments of Herbst and others with lithium compounds. The same defect had repeatedly occurred simply on account of the fact that the investigators had constantly subjected the eggs to the chemical substances during similar developmental periods.

On further expanding this line of investigation during the following ten years it was found that a great many different typical defects which occur in nature could be produced by any one method of experimental treatment—for example, low temperature, provided the eggs were subjected to the treatment during different developmental stages. On the other hand it was repeatedly shown that a great variety of treatments may produce only one and the same defect if the eggs be subjected to these treatments at the same developmental period, as was first recorded for a number of anesthetic substances in inducing the eye defects of Fundulus in 1909 and 1910. As stated then:

> Eye defects, in fish embryos at least, are produced by lessening the developmental energy at certain critical stages. This is readily accomplished by treating the developing embryo with anesthetics.[3]

These facts made it certain that the action of the chemical substance itself was not specific in modifying vertebrate development, and this was rapidly and further confirmed by McClendon and a number of other workers on a variety of embryos. Thus it is the embryonic stage at which the treatment is applied which determines the type of response and not the nature of the treatment.

There are critical and passive moments in the development of the embryonic organs which are associated with the fact that a certain part or organ is in an active or rapid state of development at a given time, while at other times this part may be developing more slowly or possibly be in a state of rest, and at such a time the given part is not readily affected by modifications in the environment. The critical stage is the time at which the particular organ is developing at its highest rate and probably at a rate higher than any other point in the embryo at this exact period. The experimental treatment when effective causes the embryo to react by slowing or lowering its general rate of development and the most rapidly active part is most affected; in other words, the treatment acts very much as an anesthetic would, and lack of oxygen and low temperatures, as Loeb, Kellicott and many others have found, slow the developmental activities in the same way. Thus, generally speaking, most defects are the result of developmental arrests as

[3] Stockard, *Proc. Soc. Exp. Biol. and Med.*, 7: 2. 1909.

Dareste believed, without wide experimental evidence, as long ago as 1891.

When a particular organ is once arrested or slowed in its development it is subsequently unable to overcome this handicap on account of the fact that some other organ has now reached a point in its development or ripeness when its high rate of activity enables it to dominate the situation, and this new organ itself may then tend to inhibit the development of other organs. The idea of such competitive actions among the developing organs has long been discussed in both animals and plants.

Any occurrence which tends to cause an abnormally slow rate of development will almost invariably produce an anomalous structural condition. Newman in 1917 showed in a most striking way that hybrid fish embryos actually exhibit the same types of abnormalities that are obtained by other experimental procedures, and he clearly interpreted these as being of the nature of developmental arrests, or in other words, the result of the slow hybrid development.

Changes in rate of development and different rates of cell multiplication may be clearly observed and appreciated, and it seems certain that these changes determine the type of structural reaction. The natural causes of the changes in the rate we do not know. But making tests to demonstrate that a rapidly growing part is metabolizing rapidly or oxidizing rapidly is about comparable to finding that an engine running at high speed is burning more fuel in a given time than one going slowly. We have long known that speed costs something and fast living is reputed to be somewhat more expensive than slow.

All the explanations regarding the relation of one developing organ to another actually in a sense go back a hundred years to the old ideas of Geoffroy St. Hilaire in his "balancement des organs," as well as more recently to Wilhelm Roux's "Kampf der Teile."

Not only does an inhibition of developmental rate induce abnormal expression in an organ of the single embryo, but almost ten years ago I found experimentally that an arrest during very early stages of development may actually cause more than one embryonic body to arise on the germ-ring, and thus twins or multiple vertebrate embryos may be produced. In these double embryos the competition between the two components is strikingly shown, the superior development of the one will constantly tend to inhibit the other.

It further seems very probable that this occurrence of twinning is more readily induced in one species of embryo than in another, in other words, there is a constitutional or genetic background affecting the readiness of this reaction—for example, among fish the trout embryo tends to double or form twins much more easily than do the embryos of the minnow, Fundulus, while on the other hand possibly Fundulus tends more readily than the trout to give the cyclopian defect.

Most important analogies to these phenomena have arisen in the genetic studies of the expression of certain mutations in modified environments. Miss M. A. Hoge in 1915 found an important influence of low temperature on the expression of a Mendelian character. When a definite mutant line of Drosophila was kept at low temperature, accessory and double legs were inherited in an exact Mendelian ratio. In the double legs one component tended to be a mirror image of the other, thus a typical twin extremity. However, when this line of flies was bred at normal temperatures the double legs did not occur in the Mendelian ratio. The slow development at low temperature was necessary in order to obtain the full expression of this genetic character! Of course the ordinary lines of Drosophila lacking this mutant character do not develop accessory legs in these low temperatures. Morgan recorded a similar behavior in the inheritance of abnormal abdomen in flies as associated in expression with a humid environment.

These environmental influences on the development or expression of a character in an individual emphasize the important fact that the absence of a character in a person does not at all mean the absence of the necessary factors from the germ. There is the double problem of transmission and expression; a character may be inherited but on account of unfavorable developmental conditions it does not develop or may be suppressed. The child may inherit the mouth shape of its parents and yet may exhibit hare-lip and cleft palate. As Morgan again remarks,

> In cases where, on the factorial hypothesis, a certain factor is expected to be present in an individual, then, even if the individual fails to develop the character commonly taken as indicative of the factor, the actual presence of the factor may be demonstrated by breeding tests.

If circumstances are provided like those in which the character previously appeared it will show itself again. With a race of guinea-pigs I have found this to be true even for the five-toed character which has probably been unexpressed for hundreds of years or generations since all wild guinea-pigs express only four front and three hind toes.

The studies on the modification of the developing embryo and its rather definite responses led to attempts to modify the germ cells of parent generations with the idea that such changes might be recognized by altered growth and development in the progeny and by possible transmission. My own experiments along these lines were conducted through a number of years on a great many individuals, but unhappily the treatments used failed to produce localized or limited modification in either the germ cells or the subsequent offspring. The more severe treatments did, however, produce a generalized injury to both male and female germ cells and caused very definite discrepancies between the histories of the experimental generations and the control animals. All these deficiencies in development were such as would be expected to result from general injury to the germ cell rather than from a limited or specific modification. Other workers have been more successful and, in particular Little and Bagg, by treating mice with X-rays seem to have produced a strain of animals which consistently transmit developmental abnormalities.

Here again the type of abnormality is more in the nature of what one might expect to result from a general injury to germ plasm rather than to a specific modification of any exact or definite nuclear part. However, the abnormalities, such as defective kidneys and deformed feet, seem to be definitely transmitted through a number of generations.

Finally, with X-ray experiments, Mavor, and still more accurately Muller, have succeeded in actually affecting certain definite factors or, morphologically speaking, genes in the germ cells of the fruit fly, Drosophila. In Muller's experiment in particular it seems clearly shown that the X-ray has actually caused changes in certain genes giving rise to mutant conditions that are inherited in definite Mendelian ratios. Even here the new characters resulting from these modifications might all be thought of as defects or deficiency responses in spite of their accurate inheritance. However this may be, it is highly important and stimulating to find that hereditary factors themselves may be subjected to experimental modification and analysis. This becomes an attack on the most minute morphologic unit of which we have ever conceived.

While many of the foregoing conceptions were being developed physiologists as well as morphologists were recognizing the fact that certain peculiar substances, hormones, produced within the organism were capable of modifying its morphological characters and actually, in many ways, directing the structural end pattern. Lillie's enlightening studies of the freemartin calf showed how during early intrauterine development the hormones produced in one fetus may completely alter the normal structural development of his sister twin. This study also impresses us with the importance of the very early production of a specific organ hormone and its rôle in directing structural response. The classical embryological experiments with the thyroid now so extensively confirmed leave no doubt of the necessity of the thyroid hormone as a stimulant for structural metamorphosis and development.

The chemical nature of the individual hormone produced by a given gland, such as that from the thyroid, seems to be closely the same throughout the vertebrate kingdom, but the action of this common stuff in each vertebrate species plays upon a different constitutional complex of genetic factors and brings about a varying series of specific reactions.

In the embryonic body Spemann has recently recognized the existence of what he terms "organizers," closely suggestive of hormones. Such substances seem to act on the embryonic cells or groups of cells in such a way as to harmonize development and bring about an orderly expression of the systems of the embryo. One of the striking results from the valuable experimental work which has been done on the rôle of these "organizers" is the demonstration that when a group of cells taken from a certain region of the body of the embryo of one species is planted in a different part of an embryo of another species, this group of cells is induced to develop into the exact organ which should occur in the position at which it was planted, but in spite of this it is also found that the foreign tissues nevertheless retain the species characteristics of the embryo from which they were originally taken. Although the "organizers" have the power to cause embryonic cells to form an organ proper for the place, the same "organizers" are quite unable to modify the factorial complex which gives to these cells the characteristics of their mother species.

Such results are closely in harmony with the very clearly expressed idea of Morgan, that "differentiation is due to the cumulative effect of regional differences in the egg and embryo, reacting with a complex factorial background that is *the same in every cell.*" Thus the regional differences have something associated with them which brings about differentiation without actually modifying the complex factorial background of the cells. It is certain that since every cell of the body has the same factorial or genetic complex, these factors can not cause differential reactions in development. But it is equally certain that during early cleavage the different cells very soon lie in such positions that almost all of them experience slight differences in environmental contacts—some cells lie almost entirely at the surface and others almost entirely within the blastula; these slight environmental differences acting on the common genetic complex may cause the production within the various cells of different chemical substances and these would give different growth reactions which steadily increase their differences as development progresses. These reactions bring about the changing internal environments which have originally resulted from the outer environmental contacts. When outer environments are altered, differentiation should be altered and this is true as is demonstrated by anomalous developments in modified surroundings.

Our present view is a considerable advance over the old proposition of Driesch, which, however, was partly correct, that the development of a cell is a function of its position. Driesch of course at that time knew very little of the exact genetic constitution of the cell and the interplay between this and the environment.

The old efforts to analyze promorphology and the peculiar differences in the reaction of blastomeres from the embryos of various species made it impossible to fully reconcile all the apparent developmental contradictions which arose, and finally, as Jennings recently deplores, this caused Driesch to despair of an experimental solution and to fall into the pit of metaphysical speculation. But as Jennings[4] goes on to say:

> We find that we can not naively transfer the results and principles that we obtain by experimenting on one organism to another organism; or even to another part of the same organism. We find that what one organism can't do, another can. We find that what a given organism doesn't usually do, it may do when put to it.

In view of these difficulties, morphology has reached the stage where its problems must be considered only in the light of the hereditary constitution of the organism and the reactions that this may give during the various stages of development with the changing internal and external environments. The modifications of these reactions during all the developmental periods from fertilization to manhood must be studied and analyzed in order that the actual differences between a normal man and an acromegalic giant may be expressed with an approach to scientific accuracy.

Perhaps the experimental studies of the chemical and physical environment as affecting the embryo should aid in preparing the way for a final conception of the action of hormones and internal chemical disturbances on postnatal growth and development. The metamorphosis of puberty and the functional changes associated with it, youthful growth and senility itself are all morphological reactions to environmental change. And actually the vitamins—that strange group of substances probably related to the hormones but supplied by the outer environments—are also found to be intimately concerned in influencing structural reactions during development. The splendid work of Evans along these lines has not only given us valuable knowledge of the influences of vitamins on the early processes of reproduction but has also afforded through morphological response the recognition of a new vitamin.

[4] SCIENCE, 64: 99. 1926.

Before this point some of you may feel that I have widened the discussion of morphology entirely across the field of general biology, but on second thought I trust that it will be admitted as true that any investigation involving the development, growth or modification of living structure is a problem in morphology, and all methods, chemical, physical and physiological, applicable to an analysis of structural reactions are the tools of the morphologist.

In conclusion, I should like to recall a statement made to me years ago by a most eminent anatomist. I was undertaking the organization of an anatomical laboratory and he remarked, "You will find gross human anatomy to be scientifically bankrupt." It seems to me now that only a brief scientific stocktaking is necessary to show how richly solvent rather than insolvent this subject actually is! Gross anatomy is not bankrupt; it is simply not understood! A real understanding of gross human form and structure necessitates an accurate knowledge of the processes of heredity, a clear conception of the many phenomena which have occurred during embryonic development, a knowledge of postnatal growth and differentiation along with an appreciation of the many internal and external influences which may modify the developmental course during its various periods. An approach to such an understanding will be deeply essential for a truly scientific conception of the differences among human constitutions. From this point of view it would seem improbable that any one other than a thoroughly grounded morphologist could possibly be capable of giving a complete diagnosis of an adult constitution. With a different vantage point one might still recognize some of the more evident constitutional differences—the high spots—but an actual analysis of the important finer variations in constitution, almost all of which give typical structural symptoms, is left alone for the future anatomist!

There is even a relevant problem as to whether certain immunities of manhood as contrasted with childhood susceptibilities do result from mild infections rather than from developmental changes. The adult is not the same animal as the child—it has many additional structures and secretions and its failure to contract diseases of childhood that it has never exhibited may not in all cases be due to an acquired immunity resulting from long mild exposure so much as to a sort of species immunity, since the two ages are two different animals. There is probably in many ways a wider discrepancy in organic structure and internal environment between a senile man and a new-born baby than between an old man and an old gorilla!

Human anatomy on this basis is the outstanding morphological problem. Only the old "surgical handmaid," let us thank Providence, is bankrupt, and this fact is the actual redemption of anatomy in this country.

The trend of morphology is passing beyond the descriptive phase with its refinements of measurement and towards a comprehensive analysis of the causes underlying structural reactions.

And, as morphologists, we are fortunately able to sit-in along with the geneticist while Nature shuffles and deals the chromosomes which carry the fortunes of life to her sons and daughters. To one the cards may be stacked for all that is rich and good, while to another may be dealt deformity and disease; yet all must play these hands in the vital game of somatic development and gametic transmission.

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SCIENTIFIC EVENTS

THE NATIONAL PARK SYSTEM

A STATEMENT in regard to national parks has been made public by the Department of the Interior according to which an area of approximately three square miles of spectacular scenic beauty has just been added to the Acadia National Park, on the coast of Maine, through the acceptance by the secretary of the interior of deed covering this land. The newly added section is on Schoodic Peninsula, a bold point across Frenchman's Bay on the opposite mainland from Mount Desert Island, where the main portion of the park is located.

Authority to accept gifts of land on the neighboring mainland and to change the name of the park from Lafayette to Acadia was contained in the Act of Congress approved on January 19 of this year. The entire area of the park, now totaling fifteen square miles, has been donated to the U. S. government by prominent easterners headed by George B. Dorr, of Boston and Bar Harbor, the present park superintendent.

The largest single addition to the park system during the year was caused by the creation of the Grand Teton National Park, Wyoming, by act approved by President Coolidge on February 26, last. This park, with an area of 150 square miles, includes the famous Teton Mountains, a magnificent range that has been under consideration for a number of years for addition to the Yellowstone National Park.

The Yellowstone itself was increased by the addition of seventy-eight square miles on its north and east boundaries, to take in the headwaters of the Lamar River. No roads, hotels or camps will be constructed in this new section of the park.

Lassen Volcanic National Park, in northern California, was enlarged by the addition of thirty-nine square miles of interesting volcanic territory through congressional enactment. Further legislation gave authority to consolidate or acquire alienated lands within the exterior boundaries of the park.

Bryce Canyon National Park, in southern Utah, was established on September 15, 1928, under authority previously granted by Congress. Its area is twenty-two square miles. The main feature of this park is a great amphitheater filled with innumerable fantastically eroded pinnacles of vivid coloring.

Other congressional legislation of national park interest included the enactment of a law accepting the cession by the state of Colorado of exclusive jurisdiction over the lands embraced within the Rocky Mountain National Park. The passage of the state act ceding jurisdiction ended a controversy of several years' standing between the federal and state governments.

Authority was granted for the establishment of a Bad Lands National Monument in the State of South Dakota when and if the lands necessary for inclusion are donated to the federal government.

The president of the United States was authorized to appoint a commission to study further adjustments in the boundaries of Yellowstone National Park, with special reference to the Bechler River Basin.

Authorization was also granted the secretary of the interior to investigate and report to congress on the advisability and practicability of establishing a national park to be known as the Tropic Everglades National Park in the state of Florida. The area under consideration will be inspected by government park experts next fall.

Especially important was the passage of the annual appropriation act, carrying appropriations or authorizations for expenditure for national park purposes of about $12,000,000.

APPROPRIATIONS FOR THE RESEARCH WORK OF THE DEPARTMENT OF AGRICULTURE

IN the 1930 appropriation act congress has continued the policy of expanding and strengthening the work of scientific research so as to enable the department to render greater service in this respect to farmers in every section of the country. Last year congress increased the funds for research by items totaling $1,800,000 for the work of the department