SCIENCE

FRIDAY, NOVEMBER 25, 1910

CONTENTS

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of SCIENCE, Garrison-on-Hudson, N. Y.

PROBLEMS OF ANIMAL MORPHOLOGY[1]

IN choosing a subject for the address with which it is my duty, as president of this section, to trouble you, I have found myself in no small embarrassment. As one whose business it is to lecture and give instruction in the details of comparative anatomy, and whose published work, *qualecunque sit*, has been indited on typical and, as men would now say, old-fashioned morphological lines, I seem to stand self-condemned as a morphologist. For morphology, if I read the signs of the times aright, is no longer in favor in this country, and among a section of the zoological world has almost fallen into disgrace. At all events, I have been very frankly assured that this is the case by a large proportion of the young gentlemen whom it has been my fate to examine during the past two years; and, as this seems to be the opinion of the rising generation of English zoologists, and as there are evident signs that their opinion is backed by an influential section of their elders, I have thought that it might be of some interest, and perhaps of some use, if I took this opportunity of offering an apology for animal morphology.

It is a sound rule to begin with a definition of terms, so I will first try to give a short answer to the question "What is morphology?" and, when I have given a somewhat dogmatic answer, I will try to deal in the course of this address with two further questions: What has morphology done for zoological science in the past?

[1] Address to the Zoological Section of the British Association for the Advancement of Science, Sheffield, 1910.

What remains for morphology to do in the future?

To begin with, then, what do we include under the term morphology? I must, first of all, protest against the frequent assumption that we are bound by the definitions of C. F. Wolff or Goethe, or even of Haeckel, and that we may not enlarge the limits of morphological study beyond those laid down by the fathers of this branch of our science. We are not—at all events we should not be—bound by authority, and we owe no allegiance other than what reason commends to causes and principles enunciated by our predecessors, however eminent they may have been.

The term morphology, stripped of all the theoretical conceptions that have clustered around it, means nothing more than the study of form, and it is applicable to all branches of zoology in which the relationships of animals are determined by reference to their form and structure. Morphology, therefore, extends its sway not only over the comparative anatomy of adult and recent animals, but also over paleontology, comparative embryology, systematic zoology and cytology, for all these branches of our science are occupied with the study of form. And in treating of form they have all, since the acceptance of the doctrine of descent with modification, made use of the same guiding principle—namely, that likeness of form is the index to blood-relationship. It was the introduction of this principle that revolutionized the methods of morphology fifty years ago, and stimulated that vast output of morphological work which some persons, erroneously as I think, regard as a departure from the line of progress indicated by Darwin.

We may now ask, what has morphology done for the advancement of zoological science since the publication of the "Origin of Species"? We need not stop to inquire what facts it has accumulated: it is sufficiently obvious that it has added enormously to our stock of concrete knowledge. We have rather to ask what great general principles has it established on so secure a basis that they meet with universal acceptance at the hands of competent zoologists?

It has doubtless been the object of morphology during the past half-century to illustrate and confirm the Darwinian theory. How far has it been successful? To answer this question we have to be sure of what we mean when we speak of the Darwinian theory. I think that we mean at least two things. (1) That the assemblage of animal forms as we now see them, with all their diversities of form, habit and structure, is directly descended from a precedent and somewhat different assemblage, and these in turn from a precedent and more different assemblage, and so on down to remote periods of geological time. Further, that throughout all these periods inheritance combined with changeability of structure have been the factors operative in producing the differences between the successive assemblages. (2) That the modifications of form which this theory of evolution implies have been rejected or preserved and accumulated by the action of natural selection.

As regards the first of these propositions, I think there can be no doubt that morphology has done great service in establishing our belief on a secure basis. The transmutation of animal forms in past time can not be proved directly; it can only be shown that, as a theory, it has a much higher degree of probability than any other that can be brought forward, and in order to establish the highest possible degree of probability, it was necessary to demonstrate that all anatomical, embryological and paleontological facts were consistent with it. We are apt to forget, nowadays, that there is no *a priori* reason for regarding the resemblances and differences that we observe in organic forms as something different in kind from the analogous series of resemblances and differences that obtain in inanimate objects. This was clearly pointed out by Fleeming Jenkin in a very able and much-referred to article in the *North British Review* for June, 1867, and his argument from the *a priori* standpoint has as much force to-day as when it was written forty-three years ago. But it has lost almost all its force through the arguments *a posteriori* supplied by morphological science. Our belief in the transmutation of animal organization in past time is founded very largely upon our minute and intimate knowledge of the manifold relations of structural form that obtain among adult animals; on our precise knowledge of the steps by which these adult relations are established during the development of different kinds of animals; on our constantly increasing knowledge of the succession of animal forms in past time; and, generally, on the conviction that all the diverse forms of tissues, organs and entire animals are but the expression of an infinite number of variations of a single theme, that theme being cell-division, multiplication and differentiation. This conviction grew but slowly in men's minds. It was opposed to the cherished beliefs of centuries, and morphology rendered a necessary service when it spent all those years which have been described as "years in the wilderness" in accumulating such a mass of circumstantial evidence in favor of an evolutionary explanation of the order of animate nature as to place the doctrine of descent with modification on a secure foundation of fact. I do not believe that this foundation could have been so securely laid in any other way, and I hold that zoologists were actuated by a sound instinct in working so largely on morphological lines for forty years after Darwin wrote. For there was a large mass of fact and theory to be remodelled and brought into harmony with the new ideas, and a still larger vein of undiscovered fact to explore. The matter was difficult and the pace could not be forced. Morphology, therefore, deserves the credit of having done well in the past: the question remains, What can it do in the future?

It is evident, I think, that it can not do much in the way of adding new truths and general principles to zoological science, nor even much more that is useful in the verification of established principles, without enlarging its scope and methods. Hitherto—or, at any rate, until very recently—it has accepted certain guiding principles on faith, and, without inquiring too closely into their validity, has occupied itself with showing that, on the assumption that these principles are true, the phenomena of animal structure, development and succession receive a reasonable explanation.

We have seen that the fundamental principles relied upon during the last fifty years have been inheritance and variation. In every inference drawn from the comparison of one kind of animal structure with another, the morphologist founds himself on the assumption that different degrees of similitude correspond more or less closely to degrees of blood-relationship, and to-day there are probably few persons who doubt that this assumption is valid. But we must not forget that, before the publication of the "Origin of Species," it was rejected by the most influential zoologists as an idle speculation, and that it is imperilled by Mendelian experiments showing that characters may be split up and reunited in different combinations in the course of a few generations. We do not doubt the importance of the principle of inheritance, but we are not quite so sure as we were that close resemblances are due to close kinship and remoter resemblances to remoter kinship.

The principle of variation asserts that like does not beget exactly like, but something more or less different. For a long time morphologists did not inquire too closely into the question how these differences arose. They simply accepted it as a fact that they occur, and that they are of sufficient frequency and magnitude, and that a sufficient proportion of them lead in such directions that natural selection can take advantage of them. Difficulties and objections were raised, but morphology on the whole took little heed of them. Remaining steadfast in its adherence to the principles laid down by Darwin, it contented itself with piling up circumstantial evidence, and met objection and criticism with an ingenious apologetic. In brief, its labors have consisted in bringing fresh instances, and especially such instances as seemed unconformable, under the rules, and in perfecting a system of classification in illustration of the rules. It is obvious, however, that, although this kind of study is both useful and indispensable at a certain stage of scientific progress, it does not help us to form new rules, and fails altogether if the old rules are seriously called into question.

As a matter of fact, admitting that the old rules are valid, it has become increasingly evident that they are not sufficient. Until a few years ago morphologists were open to the reproach that, while they studied form in all its variety and detail, they occupied themselves too little—if, indeed, they could be said to occupy themselves at all—with the question of how form is produced, and how, when certain forms are established, they are caused to undergo change and give rise to fresh forms. As Klebs has pointed out, the forms of animals and plants were regarded as the expression of their inscrutable inner nature, and the stages passed through in the development of the individual were represented as the outcome of purely internal and hidden laws. This defect seems to have been more distinctly realized by botanical than by zoological morphologists, for Hofmeister, as long ago as 1868, wrote that the most pressing and immediate aim of the investigator was to discover to what extent external forces acting on the organism are of importance in determining its form.

If morphology was to be anything more than a descriptive science, if it was to progress any further in the discovery of the relations of cause and effect, it was clear that it must alter its methods and follow the course indicated by Hofmeister. And I submit that an inquiry into the causes which produce alteration of form is as much the province of, and is as fitly called, morphology as, let us say, a discussion of the significance of the patterns of the molar teeth of mammals or a disputation about the origin of the cœlomic cavities of vertebrated and invertebrated animals.

There remains, therefore, a large field for morphology to explore. Exploration has begun from several sides, and in some quarters has made substantial progress. It will be of interest to consider how much progress has been made along certain lines of research—we can not now follow all the lines—and to forecast, if possible, the direction that this pioneer work will give to the morphology of the future.

I am not aware that morphologists have, until quite recently, had any very clear concept of what may be expected to underlie form and structure. Dealing, as they have dealt, almost exclusively with things that can be seen or rendered visible by the microscope, they have acquired the habit of thinking of the organism as made up of organs, the organs of tissues, the tissues of cells, and the cells as made up—of what? Of vital units of a lower order, as several very distinguished biologists would have us believe; of physiological units, of micellæ, of determinants and biophors, or of pangenes; all of them essentially morphological conceptions; the products of imagination projected beyond the confines of the visible, yet always restrained by having only one source of experience—namely, the visible. One may give unstinted admiration to the brilliancy, and even set a high value on the usefulness, of these attempts to give formal representations of the genesis of organic structure, and yet recognize that their chief utility has been to make us realize more clearly the problems that have yet to be solved.

Stripped of all the verbiage that has accumulated about them, the simple questions that lie immediately before us are: What are the causes which produce changes in the forms of animals and plants? Are they purely internal, and, if so, are their laws discoverable? Or are they partly or wholly external, and, if so, how far can we find relations of cause and effect between ascertained chemical and physical phenomena and the structural responses of living beings?

As an attempt to answer the last of these questions, we have the recent researches of the experimental morphologists and embryologists directed towards the very aim that Hofmeister proposed. Originally founded by Roux, the school of experimental embryology has outgrown its infancy and has developed into a vigorous youth. It has produced some very remarkable results, which cannot fail to exercise a lasting influence on the course of zoological studies. We have learned from it a number of positive facts, from which we may draw very important conclusions, subversive of some of the most cherished ideas of whilom morphologists. It has been proved by experiment that very small changes in the chemical and physical environment may and do produce specific form-changes in developing organisms, and in such experiments the consequence follows so regularly on the antecedent that we can not doubt that we have true relations of cause and effect. It is not the least interesting outcome of these experiments that, as Loeb has remarked, it is as yet impossible to connect in a rational way the effects produced with the causes which produced them, and it is also impossible to define in a simple way the character of the change so produced. For example, there is no obvious connection between the minute quantity of sulphates present in sea-water and the number and position of the characteristic calcareous spicules in the larva of a sea-urchin. Yet Herbst has shown that if the eggs of sea-urchins are reared in sea-water deprived of the needful sulphates (normally .26 per cent. magnesium sulphate and .1 per cent. calcium sulphate), the number and relative positions of these spicules are altered, and, in addition, changes are produced in other organs, such as the gut and the ciliated bands. Again, there is no obvious connection between the presence of a small excess of magnesium chloride in sea-water and the development of the paired optic vesicles. Yet Stockard, by adding magnesium chloride to sea-water in the proportion of 6 grams of the former to 100 c.c. of the latter, has produced specific effects on the eyes of developing embryos of the minnow *Fundulus* *heteroclitus:* the optic vesicles, instead of being formed as a widely separated pair, were caused to approach the median line, and in about 50 per cent. of the embryos experimented upon the changes were so profound as to give rise to cyclopean monsters. Many other instances might be cited of definite effects of physical and chemical agencies on particular organs, and we are now forced to admit that inherited tendencies may be completely overcome by a minimal change in the environment. The nature of the organism, therefore, is not all important, since it yields readily to influences which at one time we should have thought inadequate to produce perceptible changes in it.

It is open to any one to argue that, interesting as experiments of this kind may be, they throw no light on the origin of permanent—that is to say, inheritable—modifications of structure. It has for a long time been a matter of common knowledge that individual plants and animals react to their environment, but the modifications induced by these reactions are somatic; the germ-plasm is not affected, therefore the changes are not inherited, and no permanent effect is produced in the characters of the race or species. It is true that no evidence has yet been produced to show that form-changes as profound as those that I have mentioned are transmitted to the offspring. So far the experimenters have not been able to rear the modified organisms beyond the larval stages, and so there are no offspring to show whether cyclopean eyes or modified forms of spicules are inherited or not. Indeed, it is possible that the balance of organization of animals thus modified has been upset to such an extent that they are incapable of growing into adults and reproducing their kind.

But evidence is beginning to accumulate which shows that external conditions may produce changes in the germ-cells as well as in the soma, and that such changes may be specific and of the same kind as similarly produced somatic changes. Further, there is evidence that such germinal changes are inherited—and, indeed, we should expect them to be, because they are germinal.

The evidence on this subject is as yet meager, but it is of good quality and comes from more than one source.

There are the well-known experiments of Weismann, Standfuss, Merrifield and E. Fischer on the modification of the color patterns on the wings of various lepidoptera.

In the more northern forms of the fire-butterfly, *Chrysophanus* (*Polyommatus*) *phlœas,* the upper surfaces of the wings are of a bright red-gold or copper color with a narrow black margin, but in southern Europe the black tends to extend over the whole surface of the wing and may nearly obliterate the red-gold color. By exposing pupæ of caterpillars collected at Naples to a temperature of 10° C. Weismann obtained butterflies more golden than the Neapolitan, but blacker than the ordinary German race, and conversely, by exposing pupæ of the German variety to a temperature of about 38° C., butterflies were obtained blacker than the German, but not so black as the Neapolitan variety. Similar deviations from the normal standard have been obtained by like means in various species of *Vanessa* by Standfuss and Merrifield. Standfuss, working with the small tortoise-shell butterfly (*Vanessa urticæ*), produced color aberrations by subjecting the pupæ to cold, and found that some specimens reared under normal conditions from the eggs produced by the aberrant forms exhibited the same aberrations, but in a lesser degree. Weismann obtained similar results with the same species. E. Fischer obtained parallel results with *Arctia caja,* a brightly colored diurnal moth of the family Bombycidæ. Pupæ of this moth were exposed to a temperature of 8° C., and some of the butterflies that emerged were very dark-colored aberrant forms. A pair of these dark aberrants were mated, and the female produced eggs, and from these larvæ and pupæ were reared at a normal temperature. The progeny was for the most part normal, but some few individuals exhibited the dark color of the parents, though in a less degree. The simple conclusions to be drawn from the results of these experiments is that a proportion of the germ-cells of the animals experimented upon were affected by the abnormal temperatures, and that the reaction of the germ-cells was of the same kind as the reaction of the somatic cells and produced similar results. As everybody knows, Weismann, while admitting that the germ-cells were affected, would not admit the simple explanation, but gave another complicated and, in my opinion, wholly unsupported explanation of the phenomena.

In any case this series of experiments was on too small a scale, and the separate experiments were not sufficiently carefully planned to exclude the possibility of error. But no objection of this kind can be urged against the careful and prolonged studies of Tower on the evolution of chrysomelid beetles of the genus *Leptinotarsa. Leptinotarsa*—better known, perhaps, by the name *Doryphora*—is the potato-beetle, which has spread from a center in north Mexico southwards into the isthmus of Panama and northwards over a great part of the United States. It is divisible into a large number of species, some of which are dominant and widely ranging; others are restricted to very small localities. The specific characters relied upon are chiefly referable to the coloration and color patterns of the epicranium, pronotum, elytra and underside of the abdominal segments. In some species the specific markings are very constant, in others, particularly in the common and wide-ranging *L. decemlineata,* they vary to an extrême degree. As the potato-beetle is easily reared and maintained in captivity, and produces two broods every year, it is a particularly favorable subject for experimental investigation. Tower's experiments have extended over a period of eleven years, and he has made a thorough study of the geographical distribution, dispersal, habits and natural history of the genus. The whole work appears to have been carried out with the most scrupulous regard to scientific accuracy, and the author is unusually cautious in drawing conclusions and chary of offering hypothetical explanations of his results. I have been greatly impressed by the large scale on which the experiments have been conducted, by the methods used, by the care taken to verify every result obtained, and by the great theoretical importance of Tower's conclusions. I can do no more now than allude to some of the most remarkable of them.

After showing that there are good grounds for believing that color production in insects is dependent on the action of a group of closely related enzymes, of which chitase, the agent which produces hardening of chitin, is the most important, Tower demonstrates by a series of well-planned experiments that colors are directly modified by the action of external agencies — viz., temperature, humidity, food, altitude and light. Food chiefly affects the subhypodermal colors of the larvæ, and does not enter much into account; the most important agents affecting the adult coloration being temperature and humidity. A *slight* increase or a *slight* decrease of temperature or humidity was found to stimulate the action of the color-producing enzymes, giving a tendency to melanism; but a large increase or decrease of temperature or humidity was found to inhibit the action of the enzymes, producing a strong tendency to albinism.

A set of experiments was undertaken to test the question whether coloration changes induced by changed environmental conditions were inherited, increased or dropped in successive generations. These experiments, carried on for ten lineal generations, showed that the changed conditions immediately produced their maximum effect; that they were purely somatic and were not inherited, the progeny of individuals which had been exposed to changed conditions through several generations promptly reverting when returned to normal conditions of environment. So far the results are confirmatory of the well-established proposition that induced somatic changes are not inheritable.

But it was found necessary to remove the individuals experimented upon from the influence of changed conditions during the periods of growth and maturation of the germ-cells. Potato-beetles emerge from the pupa or from hibernation with the germ-cells in an undeveloped condition, and the ova do not all undergo their development at once, but are matured in batches. The first batch matures during the first few days following emergence, then follows an interval of from four to ten days, after which the next batch of eggs is matured, and so on. This fact made it possible to test the effect of altered conditions on the maturing germ-cells by subjecting its imagos to experimental conditions during the development of some of the batches of ova and to normal conditions during the development of other batches.

In one of the experiments four male and four female individuals of *L. decemlineata* were subjected to very hot and dry conditions, accompanied by low atmospheric pressure, during the development and fertilization of the first three batches of eggs. Such conditions had been found productive of albinic deviations in previous experiments. As soon as the eggs were laid they were removed to normal conditions, and the larvæ and pupæ reared from them were kept in normal conditions. Ninety-eight adult beetles were reared from these batches of eggs, of which eighty-two exhibited the characters of an albinic variety found in nature and described as a species under the name *pallida;* two exhibited the characters of another albinic species named *immaculothorax*, and fourteen were unmodified *decemlineatas*. This gave a clear indication that the altered conditions had produced modifications in the germ-cells which were expressed by color changes in the adult individuals reared from them. To prove that the deviations were not inherent in the germ-plasm of the parents, the latter were kept under normal conditions during the periods of development and fertilization of the last two batches of eggs; the larvæ and pupæ reared from these eggs were similarly subjected to normal conditions, and gave rise to sixty-one unmodified *decemlineatas*, which, when bred together, came true to type for three generations. The *decemlineata* forms produced under experimental conditions also came true to type when bred together. Of the *pallida* forms produced by experimental conditions all but two males were killed by a bacterial disease. These two were crossed with normal *decemlineata* females, and the result was a typical Mendelian segregation, as shown by the following table:

2 ♂ *pallida* × 2 ♀ *decemlineata*

↓

Hybrids, *decemlineata* characters dominant

5 ♂ × 3 ♀

↓ *Pallida* 6 ♂, 4 ♀ → *Decemlineata* and hybrids 16 ♂, 14 ♀

Pallida 6 ♂, 4 ♀ ↓ *Pallida* 18 ♂, 23 ♀

Decemlineata and hybrids 16 ♂, 14 ♀ → *Pallida* 8 ♂, 7 ♀; *Decemlineata* and hybrids 26 ♂, 28 ♀

This is a much more detailed experiment than those of Standfuss, Merrifield and Fisher, and it shows that the changes produced by the action of altered conditions on the maturing germ-cells were definite and discontinuous, and therefore of the nature of mutations in De Vries's sense.

In another experiment Tower reared three generations of *decemlineata* to test the purity of his stock. He found that they showed no tendency to produce extreme variations under normal conditions. From this pure stock seven males and seven females were chosen and subjected during the maturation periods of the first two batches of ova to hot and dry conditions. Four hundred and nine eggs were laid, from which sixty-nine adults were reared, constituted as follows:

Twenty (12 ♂, 8 ♀) apparently normal *decemlineata*.
Twenty-three (10 ♂, 13 ♀) *pallida*.
Five (2 ♂, 3 ♀) *immaculothorax*.
Sixteen (9 ♂, 7 ♀) *albida*.

These constituted lot A.

The same seven pairs of parents subjected during the second half of the reproductive period to normal conditions gave 840 eggs, from which were reared 123 adults, all *decemlineatas*. These constituted lot B. The *decemlineatas* of lot A and lot B were reared side by side under normal and exactly similar conditions. The results were striking. From lot B normal progeny were reared up to the tenth generation, and, as usual in the genus, two generations were produced in each year. The *decemlineatas* of lot A segregated into two lots in the second generation. A^1 were normal in all respects, but A^2, while retaining the normal appearance of *decemlineata,* went through five generations in a year, and this for three successive years, thus exhibiting a remarkable physiological modification, and one without parallel in nature, for no species of the genus *Leptinotarsa* are known which produce more than two generations in the year. This experiment is a sufficient refutation of Weismann's argument that the inheritance of induced modifications in *Vanessa urticæ* is only apparent, the phenomena observed being due to the inheritance of two kinds of determinants—one from dark-colored forms which are phyletically the oldest and the other from more gaily colored forms derived from the darker forms. There is no evidence whatever that there was ever a species or variety of potato-beetle that produced more than two, or at the most, and then as an exception, three broods in a year.

The modified albinic forms in this last experiment of Tower's were weakly; they were bred through two or three generations and came true to type, but then died out. No hybridization experiments were made with them, but in other similar experiments, which I have not time to mention in detail, modified forms produced by the action of changed conditions gave typical Mendelian characters when crossed with unmodified *decemlineatas*, thus proving that the induced characters were constant and heritable according to the regular laws.

I have thought it worth while to relate these experiments at some length, because they seem to me to be very important, and because they do not appear to have attracted the attention in this country that they deserve.

They are confirmed to a very large extent by the experiments of Professor Klebs on plants, the results of which were published this summer in the Croonian Lecture on "Alterations of the Development and Forms of Plants as a Result of Environment." As I have only a short abstract of the Croonian Lecture to refer to, I can not say much on this subject for fear of misrepresenting the author; but, as far as I can judge, his results are quite consistent with those of Tower. *Sempervivum funckii* and *S. acuminatum* were subjected to altered conditions of light and nutrition, with the result that striking variations, such as the transformation of sepals into petals, of petals into stamens, of stamens into petals and into carpels, were produced. Experiments were made on *Sempervivum acuminatum,* with the view of answering the question whether such alterations of flowers can be transmitted. The answer was in the affirmative. The seeds of flowers artificially altered and self-fertilized gave rise to twenty-one seedlings, among which four showed surprising deviations of floral structure. In two of these seedlings all the flowers were greatly altered, and presented some of the modifications of the mother plant, especially the transformation of stamens into petals. These experiments are still in progress, and it would perhaps be premature to lay too much stress upon them if it were not for the fact that they are so completely confirmatory of the results obtained by similar methods in the animal kingdom.

I submit to you that evidence is forthcoming that external conditions may give rise to inheritable alterations of structure. Not, however, as was once supposed, by producing specific changes in the parental soma, which changes were reflected, so to speak, upon the germ-cells. The new evidence confirms the distinctions drawn by Weismann between somatic and germinal variations. It shows that the former are not inherited, while the latter are; but it indicates that the germ may be caused to vary by the action of external conditions in such a manner as to produce specific changes in the progeny resulting from it. It is no more possible at the present time to connect rationally the action of external conditions on the germ-cells with the specific results produced in the progeny than it is possible to connect cause with effect in the experiments of Herbst and Stockard; but, when we compare these two kinds of experiments, we are no longer able to argue that it is inconceivable that such and such conditions acting on the germ-plasm can produce such and such effects in the next generation of adults. We must accept the evidence that things which appeared inconceivable do in fact happen, and in accepting this we remove a great obstacle from the path of our inquiries, and gain a distinct step in our attempts to discover the laws which determine the production of organic form and structure.

But such experiments as those which I have mentioned only deal with one aspect of the problem. They tell us about external conditions and the effects that they are observed to produce upon the organism. They give us no definite information about the internal changes which, taken together, constitute the response of the organism to external stimuli. As Darwin wrote, there are two factors to be taken into account—the nature of the conditions and the nature of the organisms—and the latter is much the more important of the two. More important because the reactions of animals and plants are manifold; but, on the whole, the changes in the conditions are few and small in amount. Morphology has not succeeded in giving us any positive knowledge of the nature of the organism, and in this matter we must turn for guidance to the physiologists, and ask of them how far recent researches have resulted in the discovery of factors competent to account for change of structure. Perhaps the first step in this inquiry is to ask whether there is any evidence of internal chemical changes analogous in their operation to the external physical and chemical changes which we have been dealing with.

There is a great deal of evidence, but it is extremely difficult to bring it to a focus and to show its relevancy to the particular problems that perplex the zoologist. Moreover, the evidence is of so many different kinds, and each kind is so technical and complex, that it would be absurd to attempt to deal with it at the end of an address that has already been drawn out to sufficient length. But perhaps I may be allowed to allude to one or two generalizations which appear to me to be most suggestive.

We shall all agree that, at the bottom, production and change of form is due to increase or diminution of the activities of groups of cells, and we are aware that in the higher animals change of structure is not altogether a local affair, but carries with it certain consequences in the nature of correlated changes in other parts of the body. If we are to make any progress in the study of morphogeny, we ought to have as exact ideas as possible as to what we mean when we speak of the activities of cells and of correlation. On these subjects physiology supplies us with ideas much more exact than those derived from morphology.

It is, perhaps, too sweeping a generalization to assert that the life of any given animal is the expression of the sum of the activities of the enzymes contained in it, but it seems well established that the activities of cells are, if not wholly, at all events largely, the result of the actions of the various kinds of enzymes held in combination by their living protoplasm. These enzymes are highly susceptible to the influence of physical and chemical media, and it is because of this susceptibility that the organism responds to changes in the environment, as is clearly illustrated in a particular case by Tower's experiments on the production of color changes in potato-beetles. Bayliss and Starling have shown that in lower animals, protozoa and sponges, in which no nervous system has been developed, the response of the organism to the environment is effected by purely chemical means. In protozoa, because of their small size, the question of coadaptation of function hardly comes into question; but in sponges, many of which are of large size, the mechanism of coadaptation must also be almost exclusively chemical. Thus we learn that the simplest and, by inference, the phyletically oldest mechanism of reaction and coordination is a chemical mechanism. In higher animals the necessity for rapid reaction to external and internal stimuli has led to the development of a central and peripheral nervous system, and as we ascend the scale of organization, this assumes a greater and greater importance as a coordinating bond between the various organs and tissues of the body. But the more primitive chemical bond persists, and is scarcely diminished in importance, but only overshadowed by the more easily recognizable reactions due to the working of the nervous system. In higher animals we may recognize special chemical means whereby chemical coadaptations are established and maintained at a normal level, or under certain circumstances altered. These are the internal secretions produced by sundry organs, whether by typical secretory glands (in which case the internal secretion is something additional and different from the external secretion), or by the so-called ductless glands, such as the thyroid, the thymus, the adrenal bodies, or by organs which can not strictly be called glands—namely, the ovaries and testes. All these produce chemical substances which, passing into the blood or lymph, are distributed through the system, and have the peculiar property of regulating or exciting the specific functions of other organs. Not, however, of all the organs, for the different internal secretions are more or less limited and local in their effects: one affecting the activity of this and another the activity of that kind of tissue or organ. Starling proposed the name hormones for the internal secretions because of their excitatory properties (ὁρμάω, to stir up, to excite).

Hormones have been studied chiefly from the point of view of their stimulating effect on the metabolism of various organs. From the morphologist's point of view, interest chiefly attaches to the possibility of their regulating and promoting the production of form. It might be expected that they should be efficient agents in regulating form, for, if changes in structure are the result of the activities of groups of cells, and the activities of cells are the results of the activities of the enzymes which they contain, and if the activities of the enzymes are regulated by the hormones, it follows that the last-named must be the ultimate agents in the production of form. It is difficult to obtain distinct evidence of this agency, but in some cases at least the evidence is sufficiently clear. I will confine myself to the effects of the hormones produced by the testes and ovaries. These have been proved to be intimately connected with the development of secondary sexual characters—such, for instance, as the characteristic shape and size of the horns of the bull; the comb, wattles, spurs, plumage color and spurs in poultry; the swelling on the index finger of the male frog; the shape and size of the abdominal segments of crabs. These are essentially morphological characters, the results of increased local activity of cell-growth and differentiation. As they are attributable to the stimulating effect of the hormone produced by the male organ in each species, they afford at least one good instance of the production of a specific change of form as the result of an internal chemical stimulus. We get here a hint as to the nature of the chemical mechanism which excites and correlates form and function in higher organisms; and, from what has just been said, we perceive that this is the most primitive of all the animal mechanisms. I submit that this is a step towards forming a clear and concrete idea of the inner nature of the organism. There is one point, and that a very important one, upon which we are by no means clear. We do not know how far the hormones themselves are liable to change, whether by the action of external conditions or by the reciprocal action of the activities of the organs to which they are related. It is at least conceivable that agencies which produce chemical disturbances in the circulating fluids may alter the chemical constitution of the hormones, and thus produce far-reaching effects. The pathology of the thyroid gland gives some ground for belief that such changes may be produced by the action of external conditions. But, however this may be, the line of reasoning that we have followed raises the expectation that a chemical bond must exist between the functionally active organs of the body and the germ-cells. For if, in the absence of a specialized nervous system, the only possible regulating and coadapting mechanism is a chemical mechanism, and if the specific activities of a cell are dependent on the enzymes which it holds in combination, the germ-cells of any given animal must be the depository of a stock of enzymes sufficient to insure the due succession of all its developmental stages as well as of its adult structure and functions. And as the number of blastomeres increases, and the need for coordination of form and function arises, before ever the rudiments of a nervous system are differentiated, it is necessary to assume that there is also a stock of appropriate hormones to supply the chemical nexus between the different parts of the embryo. The only alternative is to suppose that they are synthesized as required in the course of development. There are grave objections to this supposition. All the evidence at our disposal goes to show that the potentialities of germ-cells are determined at the close of the maturation divisions. Following the physiological line of argument, it must be allowed that in this connection "potentiality" can mean nothing else than chemical constitution. If we admit this, we admit the validity of the theory advanced by more than one physiologist that heritable "characters" or "tendencies" must be identified with the enzymes carried in the germ-cells. If this be a true representation of the facts, and if the most fundamental and primitive bond between one part of an organism and another is a chemical bond, it can hardly be the case that germ-cells—which, *inter alia,* are the most primitive, in the sense of being the least differentiated, cells in the body—should be the only cells which are exempt from the chemical influences which go to make up the coordinate life of the organism. It would seem, therefore, that there is some theoretical justification for the inheritance of induced modifications, provided that these are of such a kind as to react chemically on the enzymes contained in the germ-cells.

One further idea that suggests itself to me and I have done. Is it possible that different kinds of enzymes exercise an inhibiting influence on one another; that germ-cells are "undifferentiated" because they contain a large number of enzymes, none of which can show their activities in the presence of others, and that what we call "differentiation" consists in the segregation of the different kinds into separate cells, or perhaps, prior to cell-formation, into different parts of the fertilized ovum, giving rise to the phenomenon known to us as prelocalization? The idea is purely speculative; but, if it could be shown to have any warrant, it would go far to assist us in getting an understanding of the laws of the production of form.

I have been wandering in territories outside my own province, and I shall certainly be told that I have lost my way. But my thesis has been that morphology, if it is to make useful progress, must come out of its reserves and explore new ground. To explore is to tread unknown paths, and one is likely to lose one's way in the unknown.

To stay at home in the environment of familiar ideas is no doubt a safe course, but it does not make for advancement. Morphology, I believe, has as great a future before it as it has a past behind it, but it can only realize that future by leaving its old home, with all its comfortable furniture of well-worn rules and methods, and embarking on a journey, the first stages of which will certainly be uncomfortable and the end is far to seek.

G. C. Bourne

GEOGRAPHY AND SOME OF ITS MORE PRESSING NEEDS[1]

At the close of a reign which has practically coincided with the first decade of a new century, it is natural to look back and summarize the progress of geography during the decade. At the beginning of a new reign it is equally natural to consider the future. Our new sovereign is one of the most traveled of men. No monarch knows the world as he knows it; no monarch has ruled over a larger empire or seen more of his dominions. His advice has been to wake up, to consider and to act. It will be in consonance with this advice if I pay more attention to the geography of the future than to that of the past, and say more about its applications than about its origins.

Yet I do so with some reluctance, for the last decade has been one of the most active and interesting in the history of our science. The measurement of new and the remeasurement of old arcs will give us better data for determining the size and shape of the earth. Surveys of all kinds, from the simple route sketches of the traveler to the elaborate cadastral surveys of some of the more populous and settled regions have so extended our knowledge of the surface features of the earth that a map on the scale of 1,000,000 is not merely planned, but actually partly executed. Such surveys and such maps are the indispensable basis of our science, and I might say much about the need for accurate topographical surveys. This, however, has been done very fully by some of my predecessors in this chair in recent years.

The progress of oceanography has also been great. The soundings of our own and other admiralties, of scientific oceanographical expeditions, and those made for the purpose of laying cables, have given us much more detailed knowledge of the irregularities of the ocean floor. An international map of oceanic contours due to the inspiration and munificence of the prince of oceanographers and of Monaco has been issued during the decade, and so much new material has accumulated that it is now being revised. A comparison of the old and new editions of Krümmel's "Ozeanographie" shows us the immense advances in this subject.

Great progress has been made on the geographical side of meteorology and climate. The importance of this knowledge for tropical agriculture and hygiene has led to an increase of meteorological stations all over the hot belt—the results of which will be of immense value to the geographer. Mr. Bartholomew's "Atlas of Meteorology" appeared at the beginning, and Sir John Eliot's "Meteorological Atlas of India" at the end of the decade. Dr. Hann's "Lehrbuch" and the new edition of his "Climatology," Messrs. Hildebrandsson and Teisserenc de Bort's great work, "The Study of the Upper Atmosphere," are among the landmarks of progress. The record is marred only by the closing of Ben Nevis Observatory. A comparison of the present number and dis-

[1] Address to the Geographical Section of the British Association for the Advancement of Science, Sheffield, 1910.