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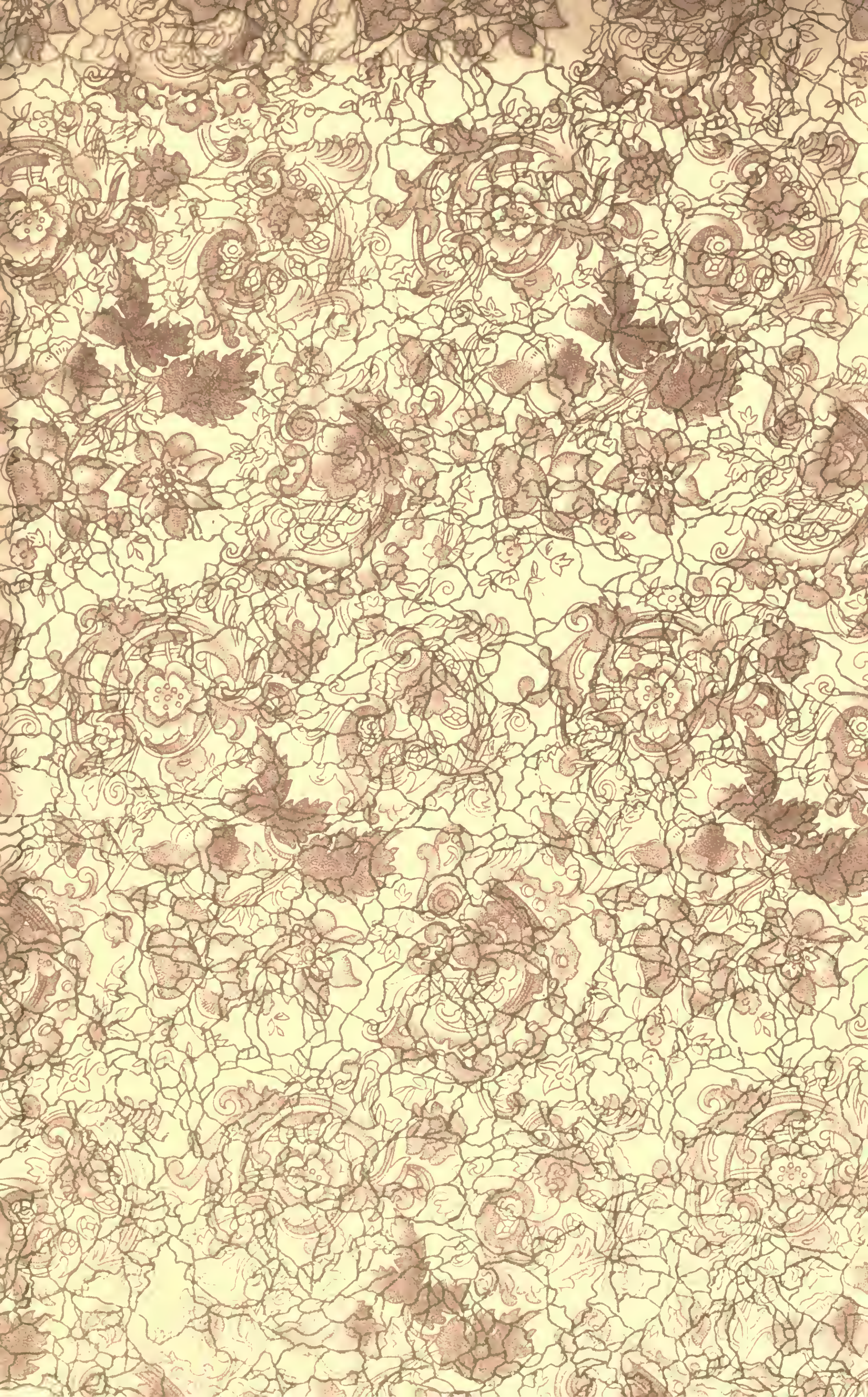


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PERSEPOLIS

Photogravure from a Painting by Briton Rivière

A picturesque display of most remarkable ruins is all that now remains of Persepolis, the capital of ancient Persia, with which, according to ancient writers, no other city could be compared either in beauty or in wealth, and which was generally designated as the "Glory of the East." Alexander the Great, in his march of conquest, destroyed some of the chief palaces, and the rest gradually fell into decay. The most important of these ruins is the Chehel Minâr (Forty Pillars). Massive double flights of steps lead to a platform strewn with ruins, from which still tower some forty colossal marble columns. These steps together with the artificial terraces are a principal feature of the ancient palaces of Persepolis.

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DIRECTOR OF CONGRESSES

VOLUME IX

BIOLOGY

COMPRISING

Lectures on Bacteriology, Embryology, Plant Morphology,
Animal Morphology, Ecology, Plant Physiology,
Plant Pathology, Human Anatomy,
Comparative Anatomy, and
General Biology

UNIVERSITY ALLIANCE

LONDON NEW YORK

ILLUSTRATIONS

VOLUME IX

TABLE OF CONTENTS

VOLUME IX

BIOLOGY

TABLE OF CONTENTS

GROUP OF INTERNATIONAL LECTURERS

The group reproduced here presents many famous lecturers of the International Congress of Arts and Science. In the front row (from left to right) are Dr. George M. Duncan, Professor of Philosophy, Yale University; Dr. William A. Hammond, Professor of Philosophy and Aesthetics, Cornell University; Dr. Ludwig Boltzmann, Professor of Physics, University of Vienna; Dr. James McKeen Cattell, Professor of Psychology, Columbia University; Dr. Wilhelm Ostwald, Professor of Physical Chemistry, University of Leipzig; Dr. James E. Creighton, Professor of Philosophy, Cornell University; Dr Harald Hoeffding, Professor of Philosophy, University of Copenhagen; Dr. Benno Erdmann, Professor of Philosophy, University of Bonn; Dr. Jacques Loeb, Professor of Physiology, University of California; and Dr. Svante A Arrhenius, Professor of Physics, University of Stockholm.

DEPARTMENT XIII — BIOLOGY

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(*Hall* 2, *September* 20, 11.15 *a. m.*)

CHAIRMAN: PROFESSOR WILLIAM G. FARLOW, Harvard University.
SPEAKERS: PROFESSOR JOHN M. COULTER, University of Chicago.
PROFESSOR JACQUES LOEB, University of California.

DEVELOPMENT OF MORPHOLOGICAL CONCEPTIONS

BY JOHN MERLE COULTER

[**John Merle Coulter,** Head of the Department of Botany, University of Chicago, Chicago, Illinois. **b.** November 20, 1851, Ningpo, China. A.B. Hanover College, 1870; A.M. *ibid.* 1873; Ph.D. Indiana University, 1890. Botanist, Hayden Survey, 1872–74; Professor of Natural Science, Hanover College (Ind.) 1874–89; Professor at Wabash College (Ind.) 1889–91; President of Indiana University, 1891–93; President, Lake Forest University (Ill.) 1893–96; Head of the Department of Botany, University of Chicago, 1896. Member, Fellow, American Association for the Advancement of Science; Botanical Society of America; Associate Fellow, American Academy of Arts and Science; Académie Internationale de Géographie Botanique. **Author of** *Synopsis of the Flora of Colorado; Manual of the Botany of the Rocky Mountain Region; Handbook of Plant Dissection; Revision of North American Umbelliferæ; Manual of the Botany of the Northern United States; Botany of Western Texas; A Synopsis of Mexican and Central American Umbelliferæ; Morphology of Gymnosperms; Morphology of Angiosperms; Plant Relations; Plant Structures; Plant Studies.*]

ANY outline of the progress of biology during the century commemorated by this Exposition that is compressed within a single address must be either inadequate or must restrict itself to some single point of view. The latter alternative must be the one chosen, not only on account of the vastness of the material, but chiefly that personal experience may give some value to the presentation. In the present address, therefore, certain limitations become necessary, and in this case they are very natural.

In the first place, it would be presumptuous in me to include zoology in any review of progress, for botanists, as a rule, are strictly limited by their material, and have never confounded botany with biology. It is true that such subjects as morphology and physiology are not to be limited by any barrier that may be set up between plants and animals, but it is also true that the material and literature with which one is familiar do not often cross this barrier. At the same time, I think it must be recognized that botany and zoölogy have been mutually stimulating, every real advance in the one having given an impetus to the other, and that, as a consequence, their progress has been largely along parallel lines. Hence a review of any phase of the progress of the one may serve as an indication of the progress of the other.

In the second place, to outline the progress of biology even from the standpoint of botany is too large a subject to be included in the grasp of any one man in such a way that he can recognize the movements in his own experience. The general botanist no longer exists except in name, and any general survey of botanical activity would have to be a compilation rather than a contribution. With these limitations, it becomes necessary for me to restrict myself largely to such an outlook as is given by plant morphology, and even then to speak only of those conclusions that come naturally to one in contact with the morphology of vascular plants. And yet I believe that a history of the development of the fundamental conceptions of plant morphology may be taken as a fair illustration of what has been going on, not only in botany in general, but also in biology.

In the third place, the period included in this survey of plant morphology need not extend beyond the middle of the last century, for at least three reasons: (1) The earlier progress of the science has been outlined by Sachs in his admirable *History of Botany;* (2) modern morphology finds its beginnings in a very real sense in the work of Hofmeister; and (3) Darwin's theory of natural selection gave the strong evolutionary impulse that it has felt ever since.

My principal theme, therefore, is the development of morphological conceptions as illustrated by plant morphology.

It would be confusing to introduce the mass of details and the names of investigators suggested by this subject. Nor would there be any advantage in recording the changes of conceptions in reference to the great variety of structures developed by the plant body and in reference to their relation to one another. My purpose is to illustrate the general change of attitude, the shifting of the point of view, in reference to plant organs, as knowledge has increased. No definite names or dates can be cited, for the movement has been general and gradual, developed out of common experience and proceeding from the background of accumulated knowledge. Disregarding the numerous possible subdivisions, the attitude of mind towards a plant organ during the last half-century has presented three distinct phases.

I. *The Phase of the Mature Organ*

At the beginning of the period under consideration, the morphologist concerned himself chiefly with completed organs, and an overshadowing rigid taxonomy compelled the idea of their classification. A few theoretical types of organs had been selected, and all organs were forced by the doctrine of metamorphosis to lie upon this Procrustean bed. All parts of vascular plants, for example, were regarded as roots, stems, or leaves under various disguises. It does not seem unreasonable to characterize this conception as the arbitrary selection of an ideal type, the natural offspring of the conception of ideal types that prevailed in taxonomy. In other words, morphology was dominated by taxonomy, and morphologists were first and chiefly taxonomists. It is this phase of morphology that must continue to be exploited chiefly by taxonomists, and which still remains in those conservative schools in which instruction lags far behind research. This doctrine of types resulted in the cataloguing of organs just as species were being catalogued, and, although capable of recording material, it was incapable of advancing knowledge.

An accompaniment of this mental attitude was the explanation of metamorphoses. It is almost impossible for one age to conceive of the mental condition that was satisfied with the explanations of a previous age. In this case it must be remembered that the earlier botanists were either ecclesiastically trained or not trained at all, and to them it was entirely satisfying to explain all metamorphoses upon teleological grounds. It is a matter of great surprise, however, to note how this point of view is still maintained by some investigators who have abandoned the doctrine of types, and in every other respect are inhaling a modern atmosphere.

One serious result of belief in the doctrine of types was the use of the most complex structures to explain the simpler ones; the reading of complexity into simplicity. For example, the type flower selected was one that had become completely differentiated; in short, a highly organized flower. This was read into all simpler flowers, and was even carried over the boundary of angiosperms and applied among gymnosperms, to the utter confusion of terminology and understanding. Fortunately for the students of cryptogams, a great gulf was thought to be fixed between plants with seeds and those without, and this the flower did not cross.

It is safe to say that this phase of morphology, with its types and teleology, and its use of complex structures to interpret simple ones, is now in its decline.

II. *The Phase of the Structure of the Developing Organ*

This type of morphology has chiefly characterized the period under consideration. Its fundamental conception is evolution; its purpose is to discover phylogeny; and its method is based upon the belief that ontogeny recapitulates phylogeny. As a consequence, there was developed for the first time what may be called a philosophy of the plant kingdom, organizing the details of morphology into one coherent whole about such central facts as alternation of generations and heterospory. Study of the metamorphoses of plant organs was replaced by a study of their development and of "life-histories," and the earliest stages of gametophyte and sporophyte and reproductive organs were scrutinized and recorded in the greatest detail in the search for relationships. Shifting its centre of gravity from the mature organ to the nascent organ, morphology departed very far from special taxonomy, while at the same time it was laying the solid foundation for general taxonomy. The reversal of old ideas was conspicuous, and much of the old terminology was found to be false in suggestion and almost impossible to shake off. For example, it has been a constant surprise to me to see the persistent use of a sex terminology in connection with flowers by those who must know better, and who must know also that they are helping to perpetuate a radical misconception.

A still more important result of this change of front in the morphological attack was the necessary reversal of the method of interpretation. No longer was the flower of highly organized angiosperms read down into the structures of the lower groups; but from the simplest beginnings structures were traced through increasing complexity and seen to end in the flower, explaining what it is. This meant that evolution had replaced the old idea of types and metamorphosis, and was building facts into a structure rather than cataloguing them. This spirit of modern morphology has not as yet dominated instruction. Its facts are developed in all their detail, abundantly and skillfully, but very seldom do the facts seem to be coördinated. The old spirit of accumulating unrelated material still dominates teaching, and crams the memory without developing permanent tissue.

The detailed developmental study of plants and their organs gave rise to what has been called morphological cytology, but it is an unfortunate differentiation, for cytology merely pushes the search for structure to the limits of technique. It is becoming more and more clear that every morphologist must also be a cytologist; and certainly every cytologist should be a morphologist; and there is no more reason for differentiation on this basis than on the basis of objectives used.

While fully recognizing the magnificent development of morphological knowledge that has resulted from this point of view, it is interesting to note running all through it much of the rigidity of the older morphology, leavened to a certain extent by the demands of evolution. Certain definite morphological conceptions were established, and organs were as rigidly outlined and defined as under the old régime. For example, there were no more definite morphological conceptions than sporangium, antheridium, and archegonium. Unconsciously, perhaps, a type of each was selected, this time from their display in the lower plant groups; and this type was read into the structure of higher groups. The distinctly outlined antheridia and archegonia of bryophytes were compelled to remain just as distinct of definition when they become confused among surrounding tissues in the pteridophytes; and the beautifully distinct sporangium of the leptosporangiates compelled the idea of an imbedded sporangium among the eusporangiates. In other words, the concept included non-essential with essential structures, a distinct wall about a sporangium being just as much a part of the definition as the sporogenous tissue, and its presence compelled even in the absence of any occasion for it. It can hardly be doubted that this was a heritage of habit from the older morphology, for it is in a sense a continuation of the conception of types. The recent morphologist who traces a sporangium wall into an anther is the same in spirit as the older morphologist who saw in the stamen a transformed leaf.

Associated with this rigidity of conception as to structure was the idea of predestination, and search was made for the cell or cell-group that was foreordained to produce a given structure. There was no idea that the fate of these cells might be changed or that other cells might share it. The repeated attempts to discover an exact definition of the term archesporium will serve as an illustration; and the repeated failures should have warned sooner than they did. Indifference of primordia was not thought of, and each living cell was conceived of as having only a single possibility.

The idea of unvarying sequence and predestination not only entered into the conception of developing organs, but also directed an immense amount of work in connection with the early embryonic stages of both gametophyte and sporophyte. So far as my own experience is concerned, it was in this connection that the conception of rigidity broke down. The multiplication of observations caused definite sequence and predestination to vanish in a maze of variations. This type of morphology was necessarily its own corrective, for rigidity could not stand before the accumulation of facts. In a sense, rigidity of conception is easier to grasp, and certainly simpler to present, than flexibility of conception, for the human mind seems to demand its knowledge in labeled pigeon-holes. This same spirit permeated the attitude of the morphologist of this period towards his ultimate purpose, for phylogeny to him was rather a simple conception. Similarity of structure meant community of descent. Such a condition as heterospory, such a structure as the seed, or such an organization as the sporophyte, was attained once for all, and the successful plant or group became the fortunate ancestor of all heterosporous plants, or spermatophytes, or sporophytes. This was phylogeny made easy. Multiplied observations showed that similarity of structure often does not indicate community of descent, and we are staggered before the possibilities of phylogeny.

The division of morphology that we have been pleased to call cytology has had the same experience. It was hoped that the more fundamental structures would show some reasonable constancy of phenomena, some rigidity in detail; but we have been confronted here again by endless variation, and hence most diverse interpretation of results.

Clearly, belief in a rigid sequence or in predestination could not be maintained; and in a real sense morphologists have been cataloguing material for study, and their real problems lie behind these endlessly variable details.

The phase of morphology just described has certainly been dominant during the last half-century, with phylogeny as its chief stimulus, and a rigidity of conception that only a multitude of facts could break down. It is a type that must always exist, as taxonomy must always exist, and it must be considered fundamental in familiarizing with material; but, perhaps, it may be said now to be at its culmination as the dominant phase.

III. *The Phase of the Influence of Changing Conditions upon the Developing Organ*

This means experimental morphology, and so far as organs are concerned its purpose is to discover the conditions that determine their structure and nature. All idea of rigidity has disappeared in the fundamental conception of the capacity of living cells to respond to varying conditions. What may be the possibilities of variations and what may be the exact conditions responsible for variations, are questions to be answered by experiment. If the oldest morphology is in its decline, and the current morphology at its culmination, experimental morphology may be said to be in its inception. It is easier to judge of a movement at its decline or culmination than at its inception, and experimental morphology as yet is fuller of promise than of performance. In any event, it was an inevitable phase when multiplied variation had broken down the conception of rigidity. The fundamental question of the possibilities of living cells is immediately confronting us; and the range of these possibilities may be considered under three heads.

(1) *The Varying Structure of an Organ.* Perhaps leaf variation, which enters so largely into taxonomy, may be used as an illustration. When, under experimentation, leaves can be made to vary from narrow to orbicular, from dissected to entire, and the exact physical condition determined that induces the result, any idea of rigidity in the form or structure of an organ must disappear. An observed narrow range of variation in nature may be regarded as an indication of the narrow range of conditions rather than of the narrow range of possible response on the part of the organ. From this point of view an organ is represented by its essentials, without reference to its non-essentials, and so we are now thinking of sporangia in

terms of sporogenous tissue, without reference to the presence or absence of a morphologically constant wall; of archegonia as axial rows of potential eggs, without concern for an exact morphological definition of the sterile jacket. The main question is, what determines the formation of sporogenous tissue rather than of sporangia; what determines the formation of eggs or sperms, rather than of archegonia and of antheridia?

(2) *The Possibilities of Primordia.* This has to do with what I have called the doctrine of predestination. It is more than a question as to the variable form or structure of an organ; it is a question as to the variable nature of an organ that may arise from a given primordium. When primordia that usually develop microsporangiate organs produce megasporangiate ones, or *vice versa;* when the same plant body produces sporangia or gametangia in response to conditions imposed by the experimenter; it becomes evident that primordia may be indifferent not only as to form, but also as to nature.

This meant a general unsettling of morphological conceptions. To find, for example, that a given cell is not set apart from its first appearance to function as an archesporial cell, but that there are as many potential archesporial cells as there are cells in an extensive tissue; and further to find that the archesporial cell when discovered by its functioning does not necessarily produce all the sporogenous tissue, is to abandon the idea of predestination and of defining structures on a rigid morphological basis.

(3) *The Origin of Species.* Probably the greatest triumph of experimental morphology thus far is that it has put the problem of the origin of species upon an experimental basis. The ability to vary and to vary promptly and widely, when considered in connection with structures used by taxonomists, means new species under certain conditions. To analyze these conditions is a problem of enormous complexity, but to have the problem clearly before us is but the prelude to its solution. There is still a tendency to call things inherent that are not apparent, but this is a habit not easily outgrown, and such a problem as the origin of species will long have its convenient category of "inherent tendencies."

Certain conclusions are inevitable as one considers the perspective opened by experimental morphology.

In the first place, it would seem that what we have called "biological laws" are also the laws of physics and chemistry, and the experimenter must be prepared to use all the refinements of method developed by physicists and chemists. Much of the work done in the name of experimental morphology is as yet crude in the extreme, and we are often left with a confusing plexus of conditions rather than with a satisfactory analysis. To grow plants, to observe certain results, and to draw conclusions, too frequently means the arbitrary or ignorant choice of one factor out of a possible score to be found in the uncontrolled conditions.

In the second place, that phase of ecology which deals with what are called "adaptations to environment" simply catalogues the materials of experimental morphology and must be merged with it. To retain it as a distinct field of work is to doom it to sterility, for it can only bear fruit as it becomes an experimental subject, and then it is experimental morphology.

In the third place, experimental morphology, with its background of physics and chemistry, is more closely related to physiology than it is to the older phases of morphology; which leads to the conclusion that the fundamental problems of morphology are physiological. We may look at the situation from either standpoint, and say that the most recent phase of morphology intrenches upon physiology, or that the boundaries of physiology must be extended enough to include morphology. To-day the two subjects are handicapped; for morphologists are not physiologists enough to know how to handle and interpret their material, and physiologists are not morphologists enough to know the extent and significance of their material. The training of the future must not differentiate these two subjects still further, but must combine them for effective results.

This modern tendency to cross old-established boundaries between subjects is evident everywhere. Physiology and chemistry have long possessed common territory; plant morphology and physiology have now found no barrier between them. This simply means that so long as we deal with the most external phenomena our subjects seem as distinct from one another as do the branches of a tree; but when we approach the fundamentals we find ourselves coming together, as the branches merge into the trunk. The history of botany, beginning with taxonomy, has been a history that began with the tips of the branches and has proceeded in converging lines towards the common trunk. The fundamental unity of the whole science, in fact, of biological science, however numerous the branches may be, is becoming more and more conspicuous. Already the old lines of classification have become confused, and one looking through any recent list of papers finds it impossible to classify them in terms of the old divisions. Investigators are now to be distinguished by particular groups of problems in connection with particular material, and all problems lead back to the same fundamental conceptions. In other words, the point of view is to be common to all investigators, and until it is common their results will not reach their largest significance.

A fourth consideration is the result of all this upon taxonomy. It seems clear to one who was originally trained in taxonomy, and who has passed through all the phases of morphology described above, that the conception of species has become so radically changed that a reconstructed taxonomy is inevitable. When the doctrine of types disappeared, and when experimental morphology showed the immense possibilities of fluctuation in taxonomic characters, the taxonomy of the past was swept from its moorings. Taxonomy must continue its work as a cataloguer of material, but to catalogue rigid concepts is very different from cataloguing fluctuating variations. To do the latter on the old basis is being attempted in certain quarters, but it soon passes the limit of usefulness and sets strongly towards the mere recording of individuals. Some new basis must be devised, and it must be a natural and useful expression of the relationships of forms as suggested by experimental morphology.

That this history of the progress of morphology, just outlined, is a fair indication of general tendencies may be illustrated from plant anatomy. This subject, not well differentiated from plant morphology among the lower groups, has developed a very distinct field of its own among vascular plants. Its early phase was that of classification, in which types of tissues were rigidly defined. This definite catalogue of tissues continued to be used after evolutionary morphology was well under way, and morphologists gradually abandoned any serious consideration of it, just as they had cut loose from the old taxonomy. In text-books the juxtaposition of morphology upon an evolutionary basis and a little anatomy upon a strictly taxonomic and artificial basis became very familiar.

Recently a second phase of anatomy has begun to appear, and we find it upon an evolutionary basis. Investigation has passed from the study of mature tissues to the study of developing tissues, and the seedling is more important to the anatomist than the adult body. As in the corresponding phase of morphology, the fundamental conception of this new phase is the theory of recapitulation, and its ultimate purpose is phylogeny. It views tissues as morphology views organs, and is attacking the same general problems. In so doing it becomes a special field of morphology, no more to be separated from it than are morphologists who study the sporophyte to be separated from those who study the gametophyte. It is simply the development of another line of attack upon morphological problems. This anatomical morphology, as it may be called, has yet to accumulate its share of results, and there is no region of morphology more in present need of investigators. From the small beginnings it has made it is evident that it must check the conclusions of the older morphology at every point. Even now no statement as to phylogeny can afford to neglect the testimony of anatomy.

This second phase of anatomy promises to be accompanied by a third, which finds its parallel and probably its suggestion in experimental morphology. In its incipient stage it is known as ecological anatomy, just as another phase of ecology preceded and then became merged in experimental morphology. Ecological anatomy can make no progress until it becomes an experimental subject, and then it is experimental anatomy, which holds the same relation to experimental morphology that evolutionary anatomy holds to evolutionary morphology. In other words, it is the same subject, with the same methods and purpose, and differing only in the structures investigated. And thus anatomy reaches the physiological basis, and as a part of morphology fills out the structures to be investigated from this standpoint.

There remains a region of ecology so vast and vague that it must be considered by itself for a time. It deals with such complex relationships as exist between soil, topography, climate, etc., on the one hand, and masses of vegetation, on the other. Just because it is vast and vague ought it to be attacked. The little incursions that have been made indicate the possibilities. It evidently includes some of the great ultimate problems. As yet it cannot define itself, for it seems to have no boundaries. Its materials were evident but entirely meaningless in the earlier history of botany, for it needed all of our progress before it could begin to ask intelligent questions. By virtue of its late birth it promises to develop more rapidly than any other phase of botany. And yet, beyond the inevitable preliminary classification of material, its real progress is measured by its experimental work conducted upon a definite physiological basis. Tentative generalizations are numerous and necessary, but they are merely suggestions for experiment. When one understands the close analysis necessary in the simplest physiological experiment, the problems suggested by this phase of plant ecology are appalling; but I see in the whole subject nothing but the largest application of physiology to the plant kingdom.

And now that the various phases of botany all seem to rest upon physiology, it must be apparent that the most fundamental problems are physiological. It is only recently that the development of plant physiology has justified this relationship. Its own history has been one of progress from the superficial towards the fundamental, from the behavior of a plant organ to the behavior of protoplasm. And here it becomes identified with physics and chemistry; and in a very real sense botany has become the application of physics and chemistry to plants.

THE RECENT DEVELOPMENT OF BIOLOGY

BY JACQUES LOEB

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I

THE task allotted to me on this occasion is a review of the development of biology during the last century. The limited time at our disposal will necessitate many omissions and will force me to confine myself to the discussion of a few of the departures in biology which have led or promise to lead to fertile discoveries.

The problem of a scientific investigator can always be reduced to two tasks; the first, to determine the independent variables of the phenomena which he has under investigation, and secondly, to find the formula which allows him to calculate the value of the function for every value of the variable. In physics and chemistry the independent variables are in many cases so evident that the investigation may begin directly with the quantitative determination of the relation between the change of the essential variable and the function. In biology, however, the variables, as a rule, cannot be recognized so easily, and a great part of the mental energy of the investigators must be spent in the search for these variables. To give an example, we know that in many eggs the development only begins after the entrance of a spermatozoön into the egg. The spermatozoön must produce some kind of a change in the egg, which is responsible for the development. But we do not know which variable in the egg is changed by the spermatozoön, whether the latter produces a chemical or an osmotic change, or whether it brings about a change of phase or some other effect. It goes without saying that a theory of sexual fertilization is impossible until the independent variable in the process of sexual fertilization is known.

The investigations of the biologist differ from those of the chemist and physicist in that the biologist deals with the analysis of the mechanism of a special class of machines. Living organisms are chemical machines, made of essentially colloidal material, which possess the peculiarity of developing, preserving, and reproducing themselves automatically. The machines which have thus far been produced artificially lack the peculiarity of developing, growing, preserving, and reproducing themselves, though no one can say with certainty that such machines might not one day be constructed artificially.

The specific and main work of the biologist will, therefore, be directed toward the analysis of the automatic mechanisms of development of self-preservation and reproduction.

II. *The Dynamics of the Chemical Processes in Living Organisms*

The progress made by chemistry, especially physical chemistry, has definitely put an end to the idea that the chemistry of living matter is different from the chemistry of inanimate matter. The presence of catalyzers in all living tissues makes it intelligible that in spite of the comparatively low temperature at which life phenomena occur the reaction velocities for the essential processes in living organisms are comparatively high. It has been shown, moreover, that the action of the catalyzers found in living organisms can be imitated by certain metals or other inorganic catalyzers. We may, therefore, say that it is now proved beyond all doubt that the variables in the chemical processes in living organisms are identical with those with which the chemist has to deal in the laboratory. As a consequence of this result chemical biology has during the last years entered into the series of those sciences which are capable of predicting their results quantitatively. The application of the theory of chemical equilibrium to life phenomena has led biological chemists to look for reversible chemical processes in living organisms, and the result is the discovery of the reversible enzyme actions, which we owe to A. C. Hill. I think it marks the beginning of a new epoch of the physiology of metabolism that we now know that the same enzymes not only accelerate the hydrolysis, but also in some cases, if not generally, the synthesis of the products of cleavage. It is not impossible that the results thus obtained in the field of biology will ultimately in return benefit chemistry, inasmuch as they may enable chemistry to accomplish syntheses with the help of enzymes found in living organisms which could otherwise not be so easily obtained.

A very beautiful example of the conquest of biological chemistry through chemical dynamics is offered by the work of Arrhenius and Madsen. These authors have successfully applied the laws of chemical equilibrium to toxins and antitoxins so that it is possible to calculate the degree of saturation between toxins and antitoxins for any concentration with the same ease and certainty as for any other chemical reaction.

We know as yet but little concerning the method by which enzymes produce their accelerating effects. It seems that the facts recently gathered speak in favor of the idea of intermediary reactions. According to this idea the catalyzers participate in the reaction, but form combinations that are again rapidly decomposed. This makes it intelligible that at the end of the reaction the enzmes and catalyzers are generally in the same condition as at the beginning of the reaction, and that a comparatively small quantity of the catalyzer is sufficient for the transformation of large quantities of the reacting substances.

This chapter should not be concluded without mentioning the discovery of zymase by Buchner. It had long been argued that only certain of the fermentative actions of yeast depended on the presence of enzymes which could be separated from the living cells, but that the alcoholic fermentation of sugar by yeast was inseparably linked together with the life of the cell. Buchner showed that the enzyme which accelerates the alcoholic fermentation of sugar can also be separated from the living cell, with this purely technical difference only, that it requires a much higher pressure to extract zymase than any other enzymes from the yeast cell.

III. *Physical Structure of Living Matter*

We have stated that living organisms are chemical machines whose framework is formed by colloidal material consisting of proteins, fatty compounds, and carbohydrates. These colloids possess physical qualities which are believed to play a great rôle in life phenomena. Among these qualities are the slow rate of diffusion, the existence of a double layer of electricity at the surface of the dissolved or suspended colloidal particles, and the production of definite structures when they are precipitated. We may consider it as probable that the cytological and histological structures of living matter will be reduced to the physical qualities of the colloids. But, inasmuch as the physics of the colloids is still in its beginning, we must not be surprised that the biological application of its results is still in the stage of mere suggestions. The most important result which has thus far been accomplished through the application of the physics of colloids to biology is Traube's invention of the semi-permeable membranes. To Traube we owe the discovery that every living cell behaves as if it were surrounded with a surface film which does not possess equal permeability for water and the substances dissolved in it. Salts which are dissolved in water, as a rule, migrate much more slowly into the living cells than water. This discovery of the semi-permeability of the surface films of living protoplasm made it possible to recognize the variable which determines the exchange of liquids between protoplasm and the liquid medium by which it is surrounded, namely, the osmotic pressure. Inasmuch as the osmotic pressure is measurable, this field of biology has entered upon a stage where every hypothesis can be tested exactly, and biology is no longer compelled to carry a ballast of shallow phrases. We are now able to analyze quantitatively such functions as lymph formation and the secretion of glands.

Recent investigations have thrown some light on the nature of the conditions which seem to determine the semi-permeability of living matter. Quincke had already mentioned that a film of oil acts like a semi-permeable membrane. From certain considerations of surface tension and surface energy it follows that every particle of protoplasm which is surrounded by a watery liquid must form an extremely thin film of oil at its surface. Overton has recently shown that of all dissolved substances those which possess a high solubility in fat, *e. g.*, alcohol, ether, chloroform, diffuse most easily into living cells. Overton concludes that lipoid substances, such as lecithin and cholesterin, which are found in every cell, determine the phenomenon of the semi-permeability of living matter.

IV. *Development and Heredity*

We now come to the discussion of those phenomena which constitute the specific difference between living machines and the machines which we have thus far been able to make artificially. Living organisms show the phenomena of development. During the last century it was ascertained that the development of an animal egg, in general, does not occur until a spermatozoön has entered it, but, as already stated, we do not know which variable in the egg is changed by the spermatozoön. An attempt has been made to fill the gap by causing unfertilized eggs to develop with the aid of physicochemical means. The decisive variable by which such an artificial parthenogenesis can be best produced is the osmotic pressure. It has been possible to cause the unfertilized eggs of echinoderms, annelids, and mollusks to develop into swimming larvæ by increasing transitorily the osmotic pressure of the surrounding solution. Even in vertebrates (the frog and petromyzon), Bataillon has succeeded in calling forth the first processes of development in this way. In other forms specific chemical influences cause the development, *e. g.*, in the eggs of starfish diluted acids, and, best of all, as Delage has shown, carbon dioxide. In the eggs of *Chætopterus* potassium salts produce this result, and in the case of *Amphitrite*, calcium salts.

From a sexual cell only a definite organism can arise, whose properties can be predicted if we know from which organism the sexual cell originates. The foundations of the theory of heredity were laid by Gregory Mendel in his treatise on the *Hybrids of Plants*, one of the most prominent papers ever published in biology. Mendel showed in his experiments that certain simple characteristics, as, for example, the round or angular shape of the seeds of peas or the color of their endosperm, is already determined in the germ by definite determinants. He showed, moreover, that in the case of the hybridization of certain forms one half of the sexual cells of each child contains the determinants of the one parent, the other half contains the determinants of the other parent. In thus showing that the results of hybridization can be predicted numerically, not only for one, but for a series of generations, according to the laws of the calculus of probability, he gave not a hypothesis, but an exact theory of heredity. Mendel's experiments remained unnoticed until Hugo de Vries discovered the same facts anew, and at the same time became aware of Mendel's treatise.

The theory of heredity of Mendel and de Vries is in full harmony with the idea of evolution. The modern idea of evolution originated, as is well known, with Lamarck, and it is the great merit of Darwin to have revived this idea. It is, however, remarkable that none of the Darwinian authors seemed to consider it necessary that the transformation of species should be the object of direct observation. It is generally understood in the natural sciences either that direct observation should form the foundation of our conclusions or mathematical laws which are derived from direct observations. This rule was evidently considered superfluous by those writing on the hypothesis of evolution. Their scientific conscience was quieted by the assumption that processes like that of evolution could not be directly observed, as they occurred too slowly, and that for this reason indirect observations must suffice. I believe that this lack of direct observation explains the polemical character of this literature, for wherever we can base our conclusions upon direct observations polemics become superfluous. It was, therefore, a decided progress when de Vries was able to show that the hereditary changes of forms, so-called "mutations," can be directly observed, at least in certain groups of organisms, and secondly, that these changes take place in harmony with the idea that for definite hereditary characteristics definite determinants, possibly in the form of chemical compounds, must be present in the sexual cells. It seems to me that the work of Mendel and de Vries and their successors marks the beginning of a real theory of heredity and evolution. If it is at all possible to produce new species artificially, I think that the discoveries of Mendel and de Vries must be the starting point.

It is at present entirely unknown how it happens that in living organisms, as a rule, larger quantities of sexual cells begin to form at a definite period in their existence. Miescher attempted to solve this problem in his researches on the salmon. But it seems that Miescher laid too much emphasis upon a mere secondary feature of this phenomenon, namely, that the sexual cells in the salmon apparently develop at the expense of the muscular substance of the animal. According to our present knowledge of the chemical dynamics of the animal body it seems rather immaterial whether the proteins and other constituents of the sexual cell come from the body of the animal or from the food taken up. The causes which determine the formation of large masses of sexual cells in an organism at a certain period of its existence are entirely unknown.

A little more progress has been made in regard to another problem which belongs to this group of phenomena, namely, how it happens that in many species one individual forms sperm, the other eggs. It has been known for more than a century that it is possible to produce at desire either females exclusively, or both sexes, in plant lice. In bees and related forms, as a rule at least, only males originate from the unfertilized eggs; from the fertilized eggs only females. It is, moreover, known that in higher vertebrates those twins which originate from one egg have the same sex, while the sex of twins originating from different eggs may be different. All facts which are thus far known in regard to the determination of sex seem to indicate that the sex of the embryo is already determined in the unfertilized egg, or at least immediately after fertilization. I consider it possible that in regard to the determination of sex, just as in the case of artificial parthenogenesis, a general variable will be found by which we can determine whether an egg cell will assume male or female character.

V. *Instinct and Consciousness*

The difference between our artificial machines and the living organisms appears, perhaps, most striking when we compare the many automatic devices by which the preservation of individuals and species is guaranteed. Where separate sexes exist we find automatic arrangements by which the sexual cells of the two sexes are brought together. Wherever the development of the eggs and larvæ occurs outside of the body of the mother or the nest we often find automatic mechanisms whereby the eggs are deposited in such places as contain food on which the young larva can exist and grow. We have to raise the question how far has the analysis of these automatic mechanisms been pushed. Metaphysics has supplied us with the terms "instinct" and "will" for these phenomena. We speak of instinct wherever an animal performs, without foresight of the ends, those acts by which the preservation of the individual or the species is secured. The term "will" is reserved for those cases where these processes form constituents of consciousness. The words "instinct" and "will" do, however, not give us the variables by which we can analyze or control the mechanism of these actions. Scientific analysis has shown that the motions of animals which are directed towards a definite aim depend upon a mechanism which is essentially a function of the symmetrical structure and the symmetrical distribution of irritability. Symmetrical points of the surface of an animal, as a rule, have the same irritability, which means that, when stimulated equally, they produce the same quantity of motion. The points at the oral pole as a rule possess a qualitatively different or greater irritability than those at the aboral pole. If rays of light or current curves, or lines of diffusion or gravitation, start from one point and strike an organism, which is sensitive for the form of energy involved, on one side only, the tension of the symmetrical muscles or contractile elements does not remain the same on both sides of the body, and a tendency for rotation will result. This will continue until the symmetrical points of the animal are struck equally. As soon as this occurs there is no more reason why the animal should deviate to the right or left from the direction of its plane or axis of symmetry. These phenomena of automatic orientation of animals in a field of energy have been designated as tropisms. It has been possible to dissolve a series of mysterious instincts into cases of simple tropisms. The investigation of the various cases of tropism has shown their great variety, and there can be no doubt that further researches will increase the variety of tropisms and tropism-like phenomena. I am inclined to believe that we possess in the tropisms and tropism-like mechanisms the independent variable of such functions as the instinctive selection of food and similar regulatory phenomena.

As far as the mechanism of consciousness is concerned, no scientific fact has thus far been found that promises an unraveling of this mechanism in the near future. It may be said, however, that at least the nature of the biological problem here involved can be stated. From a scientific point of view we may say that what we call consciousness is the function of a definite machine which we will call the machine of associative memory. Whatever the nature of this machine in living beings may be, it has an essential feature in common with the phonograph, namely, that it is capable of reproducing impressions in the same chronological order in which they come to us. Even simultaneous impressions of a different physical character, such as, for instance, optical and acoustical, easily fuse in memory and form an inseparable complex. The mechanism upon which associative memory depends seems to be located, in higher vertebrates at least, in the cerebral hemispheres, as the experiments of Goltz have shown. The same author has shown, moreover, that one of the two hemispheres suffices for the efficiency of this mechanism and for the full action of consciousness. As far, however, as the physical or chemical character of the mechanism of memory is concerned, we possess only a few starting points. We know that the nerve cells are especially rich in fatty constituents, and Hans Meyer and Overton have shown that substances which are easily soluble in fat also act as very powerful anæsthetics, for instance, chloroform, ether, and alcohol, and so on. It may be possible that the mechanism of associative memory depends in some way upon the constitution or action of the fatty compounds in our nerve cells. Another fact which may prove of importance is the observation made by Speck that if the partial pressure of oxygen in the air falls below one third of its normal value, mental activity very soon becomes impaired and consciousness is lost. Undoubtedly the unraveling of the mechanism of associated memory is one of the greatest discoveries which biology has still in store.

VI. *Elementary Physiological Processes*

It is, perhaps, possible that an advance in the analysis of the mechanism of memory will be made when we shall know more about the processes that occur in nerve cells in general. The most elementary mechanisms of self-preservation in higher animals are the respiratory motions and the action of the heart. The impulse for the respiratory action starts from the nerve cells. As far as the impulses for the activity of the heart are concerned, we can say that in one form at least they start from nerve cells, and in all cases from those regions where nerve cells are situated. But as far as the nature of these impulses is concerned we know as little about the cause of the rhythmical phenomena of respiration and heart-beat as we know concerning the mechanism of associative memory. It is rather surprising, but nevertheless a fact, that physiology has not progressed beyond the stage of mere suggestions and hypotheses in the analysis of such elementary phenomena as nerve action, muscular contractility, and cell division. Among the suggestions concerning the nature of contractility those seem most promising which take into consideration the phenomena of surface tension. The same lack of definite knowledge is found in regard to the changes in the sense organs which give rise to sensations. It is obvious that the most striking gaps in biology are found in that field of biology which has been cultivated by the physiologists. The reason for this is, in part, that the analysis of the elementary protoplasmic processes is especially difficult, but I believe that there are other reasons. Medical physiologists have confined themselves to the study of a few organisms, and this has had the effect that for the last fifty years the same work has been repeated with slight modifications over and over again.

VII. *Technical Biology*

I think the creation of technical biology must be considered the most significant turn biology has taken during the last century. This turn is connected with a number of names, among which Liebig and Pasteur are the most prominent. Agriculture may be considered as an industry for the transformation of radiating into chemical energy. It was known for a long time that the green plants were able to build up, with the help of the light, the carbohydrates from the carbon dioxide of the air. Liebig showed that for the growth of the plant definite salts are necessary, that these salts are withdrawn from the soil by the plants, and that in order to produce crops these salts must be given back to the soil. One important point had not been cleared up by the work of Liebig, namely, the source of nitrates in the soil which the plants need for the manufacture of their proteins. This gap was filled by Hellriegel, who found that the tubercles of the leguminosæ, or rather the bacteria contained in these tubercles, are capable of transforming the inert nitrogen of the air into a form in which the plant can utilize it for the synthesis of its proteins. Winogradski subsequently discovered that not only the tubercle bacteria of leguminosæ are capable of fixing the nitrogen of the air in the soil in a form in which it can be utilized by the plant, but that the same can be done by certain other bacteria, for instance, *Chlostridium pasteurianum*. These facts have a bearing which goes beyond the interests of agriculture. The question of obtaining nitrates from the nitrogen of the air is of importance also for chemical industry, and it is not impossible that chemists may one day utilize the experience obtained in nitrifying bacteria.

With the discovery of the culture of nitrifying bacteria we have already entered the field of Pasteur's work. Yeast had been used for the purposes of fermentation before Pasteur, but Pasteur freed this field of biology just as much from the influence of chance as Liebig did in the case of agriculture. The chemist Pasteur taught biologists how to discriminate between the useful and harmful forms of yeast and bacteria, and thus rendered it possible to put the industry of fermentation upon a safe basis.

In recent times the fact has often been mentioned that the coal fields will be exhausted sooner or later. If this is true, every source of available energy which is neglected to-day may one day become of importance. Professor Hensen has recognized the importance of the surface of the ocean for the production of crops. The surface of the ocean is inhabited by endless masses of microscopic organisms which contain chlorophyl, and which are capable of transforming the radiating energy of the sun into chemical energy.

Not only through the industry of fermentation and agriculture has technical biology asserted its place side by side with physical and chemical technology, but also in the conquest of new regions for civilization. As long as tropical countries are continually threatened by epidemics, no steady industrial development is possible. Biology has begun to remove this danger. It is due to Koch if epidemics of cholera can be suppressed to-day, and to Yersin if the spreading of plague can now be prevented. Theobald Smith discovered that the organisms of Texas fever are carried by a certain insect, and this discovery has had the effect of reducing, and possibly in the near future destroying, two dreaded diseases, namely, malaria and yellow fever.

It is natural that the rapid development of technical biology has reacted beneficially upon the development of theoretical biology. Just as physics and chemistry are receiving steadily new impulses from technology, the same is true for biology. The working out of the problems of immunity has created new fields for theoretical biology. Ehrlich has shown that in the case of immunity toxins are rendered harmless by their being bound by certain bodies, the so-called antitoxins. The investigation of the nature and the origin of toxins in the case of acquired immunity is a new problem which technical biology has given to theoretical biology. The same may be said in regard to the experiments of Pfeifer and Bordet on bacteriolysis and hemolysis. Bordet's work has led to the development of methods which have been utilized for the determination of the blood relationship of animals.

VIII. *Ethical and Economic Effects of Modern Biology*

The representatives of the mental sciences often reproach the natural sciences that the latter only develop the material, but not the mental or moral interests of humanity. It seems to me, however, that this statement is wrong. The struggle against superstition is entirely carried on by the natural sciences, and especially by the applied sciences. The nature of superstition consists in a gross misunderstanding of the causes of natural phenomena. I have not gained the impression that the mental sciences have been able to reduce the amount of superstition. Lourdes and Mecca are in no danger from the side of the representatives of the mental sciences, but only from the side of scientific medicine. Superstition disappears so slowly for the reason that the masses as a rule are not taught any sciences. If the day comes when the chief laws of physics, chemistry, and experimental biology are generally and adequately taught, we may hope to see superstition and all its consequences disappear, but not before this.

As far as the influence of the applied sciences on ethics is concerned, I think we may hope that through the natural sciences the ethics of our political and economical life will be altered. In our political as well as our economical life we are still under the influence of the ancients, especially the Romans, who knew only one means of acquiring wealth, namely, by dispossessing others of it. The natural sciences have shown that there is another and more effective way of acquiring wealth, namely, by creating it. The way of doing this consists in the invention of means by which the store of energy present in nature can be more fully utilized. The wealth of modern nations, of Germany and France, is not due to their statesmen or to their wars, but to the accomplishments of the scientists. It has been calculated that the inventions of Pasteur alone added a billion francs a year to the wealth of France. In the light of such facts it seems preposterous that statesmen should continue to instigate war simply for the conquest of territories. Through modern science the wealth of a nation can be increased much more quickly than through any territorial conquest. We cannot expect any change in the political and economical ethics of nations until it is recognized that the lawmakers and statesmen must have a scientific training. If our lawmakers possessed such a training, they would certainly not have allowed one general source of energy after another, such as oil-fields, coal-fields, water-power, etc., to be appropriated by individuals. All these stores of energy belong just as well to the community as the oxygen of the air or the radiating energy of the sun. Our present economical and political ethics is still on the whole that of the classical period or the Renaissance, because the knowledge of science among the masses and statesmen is still on that level, but the natural sciences will ultimately bring about as thorough a revolution in ethics as they have brought about in our material life.

IX. *Experimental Biology as an Independent Science*

If we compare the development of biology with the simultaneous development of physics and chemistry during the last twenty years, we must be impressed by the fact that during that time the great discoveries in physics and chemistry have followed each other surprisingly fast. The discovery of the law of osmotic pressure, the theory of electrical dissociation, the theory of galvanic batteries, the systematic formulation of physical chemistry, the discovery of electrical waves, the discovery of the X-rays, the discovery of the new elements in the air, the discovery of radioactivity, the transformation of radium into helium, the theory of radiation pressure, — what have we in biology that could be compared with such a series of discoveries? But I believe that biology has important discoveries in store, and that there is no intrinsic reason why it should be less fertile than physics and chemistry. I think the difference in the fertility of biology and the physical sciences is at least partly due to the present organization of the biological sciences.

General or experimental biology should be represented in our universities by special chairs and laboratories. It should be the task of this science to analyze and control those phenomena which are specifically characteristic of living organisms, namely, development, self-preservation, and reproduction. The methods of general biology must be those of chemistry, and especially those of physical chemistry. To-day general or experimental biology is represented in our universities neither by chairs nor by laboratories. We have laboratories for physiology, but to show how little interest physiologists take in general biology I may mention the fact that the editor of a physiological annual review excludes papers on development and fertilization from his report, as, in his opinion, this belongs to anatomy. On the other hand, anatomists and zoölogists must give their full energy to their morphological investigations, and have, as a rule, neither the time for experimental work, nor very often the training necessary for that kind of work. Only the botanists have kept up their interest in general biology, but they of course pay no attention to animal biology. In working out this short review of the development of biology during the last century, I have been impressed with the necessity of our making better provisions for that side of biology where, in my opinion, the chances for the great discoveries seem to lie, namely, *general* or *experimental* biology.

SECTION A — PHYLOGENY

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(*Hall* 2, *September* 21, 3 *p. m.*)

CHAIRMAN: PROFESSOR THOMAS HUNT MORGAN, Columbia University.
SPEAKERS: PROFESSOR HUGO DE VRIES, University of Amsterdam.
PROFESSOR CHARLES O. WHITMAN, University of Chicago.

THE Chairman of the Section of Phylogeny was Professor Thomas Hunt Morgan, of Columbia University, who began the proceedings of the Department with the following remarks:

"This Section of the Congress might have been given the title of evolution rather than of phylogeny; for, while phylogeny deals with an historical process, the term evolution has come to-day — largely through the work of De Vries — to include not only a study of the evolution of the past, but of evolution as it is taking place around us at the present time. This is not a formal distinction, but one that stands for a fundamental difference of method that has the most far-reaching consequences. The study of evolution as an historical question must have always been unsatisfactory, for all the doubts that darken the historical method would have left its conclusions dubious and unconvincing. Historical evolution could never have attained to the dignity of an exact science. The disrepute into which phylogenetic speculation has fallen in our own times furnishes an example of what we may expect from the method.

"When, on the other hand, the process of evolution was studied by the method of experiment, a new era opened. Darwin himself used extensively the experimental method, and his finest results have been reached in this way. Much of the general information of the breeders on which he relied, alas too often, are also the outcome of experiment, but of experiments by men incapable, in many cases, of employing the method with scientific precision.

"After Darwin, little was done in this direction, although a few names stand out as oases in a waste of speculation. Now once again, as Bateson has remarked, 'After a weary halt of forty years we have at last begun to march.' It is a pleasure as well as a great opportunity that we are to listen to-day to the addresses of two biologists who before all others have undertaken the study of evolution on a large scale by means of the experimental method. Professor De Vries has studied in Europe the evolutionary process in the American plant *Œnothera Lamarckiana;* while Professor Whitman has studied in America the evolution of the European pigeons. Political boundaries disappear before the advances of the sciences."

A COMPARISON BETWEEN ARTIFICIAL AND NATURAL SELECTION

BY HUGO DE VRIES

[Hugo de Vries, Professor of Botany, University of Amsterdam since 1878. **b.** Haarlem, Holland, 1848. Phil. Nat. Doct. University of Leyden, 1870; Sc.D. Columbia University; LL.D. University of Chicago, Jacksonville College; Postgraduate, Heidelberg, 1870–71; Würzburg, 1871–72; Privat-docent, Halle, 1877; Lecturer in Mutation Theory, University of California, 1904; Member of the Academy of Sciences, Amsterdam; National Academy of Sciences, Washington; American Philosophical Society, Philadelphia; Royal Society, London; Honorary Member of the Academies of Sciences of New York and of California, San Francisco; Corresponding Member of the Academies of Copenhagen, Brussels, Rome, Regensburg, Upsala, München, Philadelphia, Christiania; Honorary Member of the Deutsche Botanische Gesellschaft, Berlin, etc. Author of *Intracellulare Pangenesis; Die Mutations-Theorie; Species and Varieties, Their Origin by Mutation.*]

Natural selection, as pointed out by Darwin, is one of the great principles which rule the evolution of organisms. It is the sifting out of all those of minor worth, through the struggle for life. It is only a sieve, and no force of nature, no direct cause of improvement, as has so often been asserted. Its only function is to decide what is to live and what is to die. Evolutionary lines, however, are of long extent, and everywhere many side-paths are occurring. It is the sieve that keeps evolution on the main lines, killing all or nearly all that try to go in other directions. By this means natural selection is the one great cause of the broad lines of evolution.

With the single steps of that evolution, of course, it has nothing to do. Only after the step has been taken, the sieve decides, throwing out the bad, and thereby enabling the good to produce a richer progeny. The problem how the individual steps are brought about, is quite another side of the question.

On this point Darwin has recognized two possibilities. One means of change lies in the sudden and spontaneous production of new forms from the old stock. The other method is the gradual accumulation of the always present and ever-fluctuating variations. The first changes are what we now call mutations, the second are designated individual variations, or, since this term is often used in another sense, as fluctuations. Darwin recognized both lines of evolution, but his followers have propounded the exclusive part of the latter processes.

To my conviction the current scientific belief is wrong on this point. Horticultural experience and systematic inquiry seem to point in exactly the opposite direction. The evidence collected of late by Korshinsky from horticultural practice, may be regarded as inadequate for a full proof, most of the single cases being surrounded by doubt, and resting on incomplete observations. The main conclusions, however, seem to be quite clear, since they are always the same. Sudden sports cannot be denied to be the chief, and probably the sole, method of the origination of new horticultural forms.

There is, however, another, more weighty objection. The facts collected by Korshinsky pertain to varieties, and not to true species. Most of the varieties, and especially of the horticultural varieties, owe their origin to retrograde changes, to the apparent loss of some previously acquired character. Besides these, no doubt, there are other types, but these may be considered as of a degressive nature. Ancient characters, once lost, may reappear, and produce the impression of something quite new, whilst in reality they are only the reviving of some old latent quality. From a critical point of view the facts collected by Korshinsky may prove the sudden origin of new varieties by the loss of characters or by the revival of apparently lost ones; but they do not afford any cases of really progressive steps.

Systematic evidence has to guide us on this most important point. The subdivisions of the species afford the material for a closer study of progressive evolution. In some cases they comply with the type of horticultural variability, one form constituting a primary type, from which the remaining have obviously been derived. Such derivations are usually of a retrograde nature, consisting in the loss of color, of hairs, of spines, of wax on the surface, or of other distinct marks. Sometimes, however, they are degressive, indicating the reappearance of some latent peculiarity, and thereby seeming to repeat the characters displayed by some allied but distinct species.

In most of the cases, however, the relation between the lesser units, constituting a systematic species, is of another nature. They are all of equal importance. From one another they are distinguished by more than one mark, often by slight differences in nearly all their organs and qualities. Such forms have come to be designated as elementary species. Varieties they are only in the broad and vague significance of the word.

In some cases these different forms of the same systematic species are found in distant localities. The representatives of the same type from different countries or regions do not exactly agree, when compared with one another. Many species of ferns afford instances of this rule, and Lindley and other great systematists have often been puzzled by the wide degree of difference between the members of one single group.

In other instances the subspecies are observed to grow nearer to each other, sometimes in neighboring provinces, sometimes in the same locality, growing and flowering in mixtures of two or three, or even more, elementary species. The violets exhibit some widespread ancient types from which the numerous local species may be assumed to have arisen. The whitlow-grasses, or *Draba verna,* have no probable common ancestors amongst the now living forms, but they are crowded together in numerous types in the southern part of central Europe and more thinly spread all around, even as far as western Asia. There can be little doubt that their common origin is to be sought in the centre of their dominion and dispersion.

Numerous other instances could be given, proving the occurrence of smaller types within the systematic species. These subspecies are of equal importance, and obviously not derived from one another in a retrograde or a digressive way. They must be considered as having sprung from a common ancestor by progressive steps in diverging directions. Granting this conclusion, they constitute the real prototypes of progressive evolution, the actual steps by which progression is slowly going on.

Manifestly, this experience with wild plants must hold good for cultivated species, too. Once these must have been wild, and in this state they must have complied with the general rule. Hence we may conclude that, when first remarked and appreciated by man, they must already have existed of sundry elementary subspecies. And we may confidently assert that some must have been rich, and others poor, in such types.

This assumption at once explains the high degree of variability of so many cultivated species. This quality is not a result of cultivation, but, quite on the contrary, is to be considered as originally present, and one of the decisive causes, which have brought a species up to a high rank in cultivation. Apples afford an instance; they are notorious for their wide variability, but this term here only means polymorphy, indicating the existence of a large number of varieties. These are found in the wild state all over Europe, differentiated by various flavors and odors, but lacking the fleshiness which must be added to each of the differentiating marks by an appropriate culture and selection.

Alphonse de Candolle, who has made a profound study of the origin of cultivated plants, comes to the conclusion that the apple shrub must have had this wide dispersion already in prehistoric times, and that its cultivation must have commenced in ancient times nearly everywhere. From this most important statement of so high an authority we may conclude that the apples have not been taken into cultivation by man in one single type, but probably in numerous distinct elementary forms, transmitting thereby the wild variability in a most simple and direct way to their cultivated descendants.

It would take me too long to describe other examples. It is easily seen that it is at least as probable that the notorious high variability of so many of the most important cultivated plants is older than their culture, as that it is to be regarded as caused by this culture.

Directing now our attention to the selection of cultivated plants, it is manifest that this process has to start from distinct forms. Obviously the choice of the starting-point is as important as the improvement itself. Or rather, the results depend in a far higher degree on the adequate choice of the first representatives of the new race than on the methodical and careful treatment of its offspring. Unchangeable qualities determine the value of the new strain, if they were present in the chosen individual; if not, no selection can produce them.

This assertion, however, has not always been appreciated as it deserves, nor is it at present universally acknowledged as a first principle. The method of selecting plants was discovered by Louis de Vilmorin, about the middle of the last century. Before him selection was applied to domestic animals, and even on a large scale. Vilmorin applied it to his beets, in order to increase the amount of sugar in their roots. Evidently, he must have made some choice amongst the numerous sorts of beets of his time, or otherwise chance must have thrown into his hands exactly one of the most appropriate forms. But on this point, no historical evidence is at hand.

Since the time of Vilmorin, selection of agricultural plants has enormously gained in importance. Only of late, however, Rimpau and von Ruemker in Germany, and Willet M. Hays in this country, have begun to apply critical methods to the various parts of the process, in order to get a better insight. All of them have insisted upon the necessity of distinguishing between the first choice for a race and the subsequent improvement by continued selection. The choice of the most adequate varieties has to become the principle for the foundation of all experiments in improving races.

Hays clearly states the far-reaching importance of this practical rule by asserting that half the battle is won by choosing the variety which has to serve as a foundation stock, whilst the other half depends upon the selection of mother plants within the chosen variety. The choice of the variety is the first care of the breeder in each single case, whilst the so-called artificial selection takes only the second place. Half a century ago the famous Scotch breeder Patrick Shirreff taught that it is quite useless to search for starting-plants for improved races among varieties of minor value. Only the very best cultivated types yield the material for further successful improvement.

In practice, as in systematic science, it is usual to call all minor units within the acknowledged species by the same name of varieties, without regard to their real systematic relations. Complying with this custom, the principle of the choice of starting-points is called by Hays "variety-testing." This testing and comparing of varieties is one of the prominent lines of the work of the Agricultural Experiment Stations. Each state and each region, in some instances even each larger farm, wants its own variety of corn, or wheat, or other crops. These have to be sought out from amongst the hundreds of forms generally cultivated within each single botanical species. Once found, the type may be ameliorated according to the local conditions and wants, but this is a question of subsequent and subordinate improvement.

Summing up the main points of these arguments, we may state that artificial selection consists of two main principles, called variety-testing and racial improvement. Quite the same distinction has to be made in the case of natural selection, and the same double selection has to be acknowledged, whilst only the names have to be changed. Instead of variety-testing comes the choice between elementary species, instead of racial improvement the adaptation to the local conditions of the environment. Before going into a more detailed discussion of this first principle of comparison, it may be as well to consider that intermediate step between natural and artificial selection, which is called acclimatization.

Here the aim is given by man, but the selection is left to nature. Man, however, does not only point out the object, but has also to give the starting-points. The choice of the variety is directly performed by the climate. This is manifestly shown by the slow and gradual dispersion of corn in this country. The larger types are limited to tropical and subtropical regions, whilst the varieties capable of cultivation in the northern states are so, according to their smaller size and stature. They are short-lived, requiring a lesser number of days to reach their full development from seed to seed. These qualities are not the result of the cultivation or of the influence of the climate, since the smaller sorts are historically known to have grown in tropical America at the time of Columbus along with the taller types. This is especially on record in the case of the forty-days or quarantine maize. Cultivation has worked in this case as a sieve, or rather as a series of sieves with a diminishing width of meshes, the climate allowing only the shorter-lived forms to pass the meshes and to expand towards the north. Similar facts are known for wheat and many other crops, and the famous trials of Schuebeler in Norway have thrown a clear light upon the factors of this complicated process.

Artificial selection is a fact needing scientific and critical analysis, but natural selection is a fact which we may see at work in each field and in each meadow, but concerning which our real knowledge is still very incomplete. In the realm of natural selection, it has, however, become customary to indulge in hypothetical considerations. And since these have largely been applied to the side corresponding with the artificial improvement of races, I may perhaps be allowed to apply them here to that process, too, which corresponds to the variety-testing of the breeders.

As the easiest and most notorious examples we choose the whitlow-grasses, or *Draba verna*, and the wild pansies, or *Viola tricolor*. Nature has constituted them as groups of highly different constant forms, quite in the same way as wheat and corn. Assuming that this has happened long ago somewhere in central Europe, it is, of course, probable that the same differences in respect to the influence of climatic conditions will have prevailed as with grains. Subsequent to the period which has produced the numerous elementary species of the whitlow-grass, came a period of geographical dispersion. This process must have been wholly comparable with that of acclimatization. Some forms must have been more suited to northern climates, others to the soils of western or eastern regions, and so on. These qualities must have decided the broad lines of the dispersion, and the species must have been segregated according to their respective climatic peculiarities and their claims on soil and weather. A struggle for life and a natural selection must have accompanied and guided the dispersion, but there is no reason to assume that the sundry forms should have been changed by this process, and that we see them now endowed with other qualities than were theirs at the outset.

If this sketch strikes you favorably, natural selection must have played the same part in a large number of other cases, too. Indeed, it may be surmised that this has been its chief and prominent function. Taking up again our image of the sieve, we may assert that in such cases climate and soil are the sifting agents, and in this way the meaning of the image at once becomes a more definite one. Of course, next to climate and soil come the biological conditions, the vegetable and animal enemies of the plants, and other influences of the same nature.

Thus, everywhere in nature there must be a struggle for life in which closely related elementary species are competing with one another, fighting the same enemies. Some succeed, whilst others fail. Nature in this way performs her primary selection, and hence this process can be called selection between elementary species, or *inter-specific selection.*

The alternate principle could then be called the selection within the elementary species, or the intraspecific selection. It has now more closely to be considered. First of all comes the question whether it plays a prominent or only a subordinate part in nature.

This question may be reduced to another form, in which it is more accessible to direct investigation. Species, as we see them in nature, are in the main constant forms, fluctuating within distinct limits, which are not seen to be transgressed. Now the question arises, whether by artificial intraspecific selection it is possible to transgress those limits. If this were possible, we could pass from one species into another, and, by slow and gradual changes, convert a constant type into another equally constant form.

This question of the constancy is the chief side of the problem. One point is the production of a new character, the other the loss of the old one, which is assumed to have been changed into the new. Such losses, however, are exceedingly difficult to obtain. One of the most instructive examples is that of the lifetime of the sugar-beets. These races consist of biennial plants, and the whole process of their culture relies upon the heaping-up of sugar in the roots of the first year, leaving the production of the stems to the second summer. Now, this quality is far from being complete. Each year some annuals are seen in the fields. And not as rare exceptions, as accidental cases of atavism. Quite on the contrary, one per cent, or even more, is the rule, and often they go up to ten or more per cent. Selection, of course, is on this point always as absolute as may be; it has lasted half a century for the sugar-beets, and many centuries for the forage-crops. It has not been adequate to root the annuals out, and to render the biennial character pure.

So it is also with striped flowers and striped radishes, which yearly produce some unicolored samples, notwithstanding continuous and most severe selection. So it is ever in numerous other cases; everywhere the intraspecific selection is capable of producing ameliorated races, but incapable of making them as constant as wild species use to be.

Steady and regular advance of cultivated races no doubt occurs, although it is not at all so general as is often assumed. But whenever it occurs, the advance is due to a corresponding continuous improvement of the selecting methods, and not simply to repeated selection after the same method.

The truth of this assertion is most clearly seen in the case of the beets. They are usually adduced as the best proofs of what can be obtained by continuous selection. But the methods of judging the beets are steadily being improved, and they have been so, even since the time of Vilmorin.

Vilmorin's own method was a very simple one. Polarization had then not yet been discovered. He determined the specific weight of his beets, either by weighing them as a whole, or by using a piece cut from the base of the roots and deprived of its bark. Solutions of salts were made in which the beets swam, and diluted until they began to sink. In this way the heaviest beets could be selected, and it was assumed that they were the richest in sugar, too. This method has afterwards been improved in two ways. The first was to make large quantities of the salt-solution, choosing a medium specific weight, and selecting from among thousands of beets those which sank. The second was the determination of the specific weight of the sap expressed from the tissues. It prepared the way for the polarization. This principle was introduced about the year 1874 in Germany. It allowed the amount of sugar to be measured directly and with very slight trouble. Thousands of beets could yearly be tested, and the best chosen for the production of seed. The technical side of these determinations has since been steadily and rapidly improved. In some factories the exact determination of three hundred thousand polarization-values is effected within a few weeks.

It would take me too long to go into further details, or to describe the simultaneous changes that have been applied to the culture of the *élite.* The detailed features suffice to show that the chief care of the breeder in this case is a continuous amelioration of the method of selecting. To these great technical improvements it is manifest that the progress of the race is in the main due, and not solely to the repetition of the selection.

Similar facts may be seen on all the great lines of industrial selection. And whenever the method has reached its height, the race is soon surpassed by another, started from another varietal choice, or selected according to a better principle.

Applying this experience to the processes which are assumed to occur in nature, we may obviously assert that only in cases of a continuous change of the life-conditions in one and the same direction any real improvement of races may be expected. All other cases will only be capable of yielding local races, and such, no doubt, are very numerous. Selection keeps up the qualities some degrees above the standard of the species, and it must do so for one strain in one sense and for others in diverging directions. These local races, however, will always remain dependent upon their specific life-conditions, and never become constant in this sense of the word, that the assumed qualities should become independent specific marks. Even continued environmental changes do not seem to be adequate to produce lasting improvements.

Until now we have simply contrasted the mutations and the fluctuations. I have tried to show that both of them are subjected to selection, as well artificial as natural. In nature, and in the long run in practice too, the selection of the products of mutations plays by far the largest part. Selection of the products of fluctuating variability gives rise to inconstant, and therefore only temporary races. In practice the process is called improvement, in nature it produces the local adaptations and local races. It is not known to yield any permanent and independent results, the real results remaining always dependent on the permanency of the agency of the selective process itself. Thus interspecific selection is the broad base of progress at large, as well in practice as in nature, whilst intraspecific selection is the base of highly valuable but local and transient improvement.

This principal difference between mutative and fluctuative selection can be supported by a critical examination of the processes of fluctuation themselves. Fluctuations are the responses of the individual plants to the outward influences to which they are subjected. Of old, all these factors were thrown together under the name of nourishment, and already a century ago, Knight has pointed out how largely the variability depends on this factor. Since then, the term nourishment has been replaced by that of life-conditions, which is, of course, more appropriate on closer analysis.

Light and space, soil and water, temperature, and numerous minor factors, determine the growth of the plant and of all its parts. Quite obviously the development must depend upon them, and at least a large part of the observed fluctuating variability finds its cause and its explanation in these influences. It is readily granted that in observations of plants and animals, taken from their native localities, these influences are liable to escape the observer. In the experiment garden, however, exactly the same fluctuations occur, and statistical studies find a material, which is in no way inferior to that which is afforded by nature. Here the climatic conditions are daily seen at work. The differences in soil and manure, in space and exposure, are in large part dependent on the conscious will of the experimenter. Partly, of course, they escape his direction, but even then they are followed and controlled with utmost care, not to say with great anxiety. In the same bed one individual is affected by them in this way, and another in a diverging direction, but these relations, though often unavoidable, are commonly obvious, at least in their main features. Thence it comes that the experimenter is strongly impressed by the dependency of fluctuations on outer conditions, whilst the observer takes the variability as a fact of dubious and hypothetical explanation.

In our gardens we observe our plants during the whole period of their development. At each moment they undergo the influences of the prevailing conditions. But it is evident that each part of the plant must respond to them in its own way. One branch may be exposed to the sun, whilst others are more or less shaded. The first will enjoy all the effects of full light and vigorous assimilation, whilst the latter have only a scant supply of organic food. On richer branches the flowers will be more numerous and larger, and their variable parts produced in greater abundance. On the poor sides reduction must be the rule.

It seems quite superfluous to work out this discussion any further. It leads directly to the conclusion that fluctuating variability is, at least in large part, a process in which the various organs of a plant act more or less independently. This form of variability is therefore to be distinguished by the term of "partial fluctuation."

Opposed to it stands the individual variation, which affects the whole individual in the same manner, but which influences different individuals in different degrees and ways. If this individual fluctuation is a response to outer influences too, the question arises, when do they work, and at which period of its development does the organism respond to them.

Here for our discussion plants afford great advantages over animals. For it is clear that, as soon as buds are produced, partial fluctuation must prevail and individual variation become reduced. Therefore only the embryonic stage pertains to the latter, whilst the whole subsequent life is ruled by partial responses. The embryo itself leads its life within the seed, and thus we are induced to consider the period of the ripening of the seed as one of prominent significance for the whole group of phenomena collected under the name of fluctuations.

The life of the germ commences with the copulation of the male and female sexual cells. Obviously even these must vary, since they have been previously subjected to varying conditions. The individual characters of a given organism must, therefore, largely depend upon the degree of development of latent qualities, already present in the sexual cells before their copulation. And it is equally manifest that at that important moment there is as yet no room for partial fluctuation.

As soon, however, as tissues are developed, the chances for the latter arise and rapidly increase, whilst in the same degree the part of the individual variability must decrease. Leaving aside the buds in the axils of the cotyles, and equally discarding the primary root, we may limit our interest to the terminal vegetative cone of the young plant, and consider all variations therein provoked as of individual nature.

But as soon as this cone begins to differentiate itself, individuality comes to an end, at least in respect to the responses to varying agents, and partiality takes its place. In the same measure the embryonic life is replaced by that of the developing plant. Thus we might call the individual fluctuation by the name of embryonic fluctuation, if it is only rightly understood that the variations of the paternal and maternal cells before their copulation are to be included.

In horticultural practice individual and partial fluctuation play a very large part. Excluding the embryonic stage from the process of multiplication, the embryonic variability may be excluded, too. Hence the almost universal use of vegetative multiplication in all cases where it is practically applicable. Perennial plants and shrubs and numerous fruit trees owe their large number of varieties, and the high degree of constancy of all the samples, even, to this exclusion of one of the two main parts of the common variability. The term variety is often taken as indicating only one single individual with its peculiar characters acquired in the embryonic stage, which remain unchanged in the thousands and in the millions of its grafts and cuttings.

Nature, of course, makes some use of vegetative multiplication, too. But since this process does not play any prominent part in the current theories concerning the larger features of progressive development, it has no further interest for our present discussion.

One main point, however, has to be considered. It is seen by looking at the question from the opposite side. In order to take a definite example, we may ask to what extent an observed character is due to embryonic variability, and which part falls to the partial variability. In all cases of branched plants there is no difficulty, and every one will grant that only the average of all the leaves or all the fruits or all the flowers can be the result of embryonic changes.

But in the case of main stems and main roots there is no possibility to determine this average. An annual plant has one main stem, whilst a perennial species has many of them. The one stem is obviously to be considered as equivalent to only one of the many in the latter case. It may be of average height, but it may as well be a more or less extreme variant.

Exactly so it is in practice. The amount of sugar in an individual sugar-beet is partly due to embryonic variability and partly to the subsequent influence of treatment and weather. Now it is manifest that both are of value for the direct industrial purposes, but it is equally manifest that both cannot have the same signification for the value of the seeds which this individual plant may afterwards produce. Or, in other words, the sugar-amount of a beet is in no way a full and reliable indication of its value as a seed-bearer. If a high amount of sugar is due to embryonic variability, it is indicative of high excellence, and will probably be followed by the production of seed of primary quality. If, on the other hand, the percentage figure is reached by exceedingly favorable weather, or by an accidentally good position of a plant on the field, as to light, space, and the escape from all its enemies, it is no indication at all of embryonic variability, and it is very dubious whether it is to have a lasting influence on the seed. In fact, such a relation is strongly denied by Rimpau, von Ruemker, and other German authorities, whilst it was believed in by the famous English wheat-breeder Hallett.

Granting the exactness of the first view, the sugar-percentage figures are seen to be reliable only when subsequent or partial variability is sufficiently excluded. A hundred of selected beets may be relied upon, if used for the continuance of a single strain, but each single beet of high percentage should be regarded with doubt. Direct experiments of Laurent, of Kuhn at Naarden, and others have proved the validity of this conclusion, showing that the progeny of extreme variants does not necessarily give always high averages for the amount of sugar.

Regression has as yet chiefly been studied by means of statistical methods. It seems probable that it is largely due to the combination of embryonic and partial variability. If the latter has no influence, or only a very small influence, upon the embryonic latent qualities of the new seeds, there must be regression, even if embryonic variability itself should not be liable to it.

Turning now to the processes in nature, we may assert that the result of the struggle for life depends on the qualities of the individuals, but not on the causes of this quality. Any advance gained by partial variability will be of equal value as the same advance gained by embryonic fluctuation. Taking the latter as heritable, and the first as not, or nearly not, it is easily seen that the relation between the struggle for life and the hereditary qualities is by far not so intimate as has hitherto been assumed.

It may readily be granted that the fittest survive. But it may also be granted that, in broad figures, half of the fittest have the power to transmit their fitness to their offspring, whilst the other half have not. And if, perchance, the same proportion should hold good for the unfit, it would be of no avail for the next generation, whether it springs from the fitter or from the less fit parents.

Probably no breeder and no physiologist would take such an extreme view. Some effect of the struggle for life in nature must as well be granted as for artificial selection. My discussion had only the aim of convincing you that there is much exaggeration in the current conceptions concerning the effects of natural selection through the struggle for life between individuals of the same species. My chief object was to show that a clear distinction between embryonic and partial variability points to a prominent part of the latter and to a lesser chance of fluctuation at large playing a notable rôle in the evolution of the whole animal and vegetable kingdom.

If the visible characters of an extreme variant are no reliable base for the judgment of its hereditary excellence, the question of course arises, what marks have to be put in its place.

Obviously this is a most vital question. It is equally important from a practical point of view as with a view to the whole problem of the part of fluctuating variability in organic evolution.

It has been answered in one and the same way by practical breeders and by purely scientific experiments. Hays in this country and von Lochow in Germany have propounded the idea that the fact of heredity itself is the only fully reliable proof of heredity. Or, in other words, the average constitution of the offspring is the mark which gives us the information wanted. No visible quality can be a trustworthy substitute for it, and such are only to be regarded as surrogates.

This average constitution must be expressed by the hereditary percentage of true inheritance of the mark under consideration. If it is determined by the culture of one hundred children of each mother plant, it constitutes the centgener power of that mother, as it is called by Hays. Selection has to rely on this percentage-figure, and the results, already attained, give proof that here a new method is given which is able to yield large and rapid improvements. It is the same principle which since the earliest times is, in the main, ruling the selection of our domestic animals.

If this principle should prevail and come to exclude the selection on the ground of the visible qualities of the individuals, the comparison between artificial and natural selection will largely change its aspect. For it is evident that the latent hereditary possibilities of an individual have no influence at all on its chance of surviving in the struggle for life. Only by very remote considerations would it be possible to uphold the significance of this, but in all ordinary cases, this significance for the improvement of the race would be reduced to nothing.

Thus we see that a close analysis of the factors which provoke the fluctuating variability goes to prove how uncertain the basis is, which it affords for an explanation of organic evolution at large. On many points, artificial and natural intraspecific selection have been compared, but nowhere is this comparison favorable to the current theoretical views. On the other hand, the artificial processes of variety-testing and the theoretical and presumable selection between elementary species in nature seem to be perfectly comparable. The large practical significance of the first points clearly to an equally large theoretical importance of the latter. Hence we conclude that interspecific selection through the struggle for life is the always-acting sieve which keeps evolution on the main lines, and which in this way is the one great Darwinian cause of all organic progress.

THE PROBLEM OF THE ORIGIN OF SPECIES

BY CHARLES OTIS WHITMAN

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THE problem of problems in biology to-day — the problem which promises to sweep through the present century as it has the past one, with cumulative interest and correspondingly important results — is the one which became the life-work of Charles Darwin, and which cannot be better or more simply expressed than in the title of his epoch-making book, — *The Origin of Species.*

Darwin certainly made this problem one of universal interest, and no one will deny that the work which he did has revolutionized both the morphological and the physiological branches of biology. Indeed, no field of thought has escaped the leavening influence of his conclusions.

The prevailing belief up to Darwin's time that species were immutable forms, each separately designed and fashioned by the Creator, and each endowed with all its instincts and equipped with a structural organization perfectly adapted to its prescribed sphere of life, — this old belief was certainly effectually exploded, and is now passing into oblivion.

With one mighty stroke Darwin released biology from the thralldom of supernaturalism. In the place of special creations and cataclysmal revolutions, he set up progressive evolution through the operation of simple natural laws. To unveil that sacred mystery of mysteries, and reduce it to the level of natural laws, was a shock to all Christendom. The idea of a self-regulating, progressive evolution of species appeared, even to many eminent men of science, to be a "heresy." This was the case with Sir John Herschel, and even Sir Charles Lyell was at first of the same opinion, although he soon became convinced that natural laws were just as efficient and uniform in operation in the organic as in the inorganic world.

The outcome is familiar history. The sciences all the way up to psychology have experienced a wonderful renascence, and the world at large has moved forward in sympathetic accord to the close of a truly "Wonderful Century."

Few, however, would now claim that Darwin's solution was entirely conclusive and complete. From the nature of the case, Darwin could not exhaust the problem, and no one has made this clearer than Darwin himself, who examined his own theory with such critical acumen and breadth of knowledge that he anticipated nearly every important objection that has since been urged by others. A problem that is at once the focal point of each and every one of the biological sciences is not to be exhausted by one man, however long and successful his work. The problem has grown larger rather than smaller with every new contribution to its solution. The expansion of its horizon, however, has not, and, as I believe, is not likely to disclose the "death-bed of Darwinism." We have heard the predictions, but have witnessed no fulfillment.

Among the rival theories of natural selection two are especially noteworthy. One of these is now generally known as *orthogenesis.*[1] Theodore Eimer was one of the early champions of this theory, basing his arguments primarily upon his researches on the variation of the wall-lizard (1874–81). Eimer boldly announced his later works on *The Origin of Species* (1888), and the *Orthogenesis of the Butterflies* (1897), as furnishing *complete proof of definitely directed variation, as the result of the inheritance of acquired characters, and as showing the utter "impotence of natural selection."* Eimer's intemperate ferocity toward the views of Darwin and Weismann, coupled with an almost fanatical advocacy of the notion that organic evolution depends upon the inheritance of acquired characters, was enough to prejudice the whole case of orthogenesis. Moreover, the controversial setting given to the idea of definitely directed variation, without the aid of utility and natural selection, made it difficult to escape the conclusion that orthogenesis was only a new form of the old teleology, from the paralyzing domination of which Darwin and Lyell and their followers had rescued science. Thus handicapped, the theory of orthogenesis has found little favor outside the circle of Eimer's pupils.

The second of the two theories alluded to is the mutation theory of Hugo de Vries. The distinguished author of this theory, whose presence honors this International Congress, and lends special *éclat* to the Section of Phylogeny, maintains, on the basis of long-continued experimental research, that species originate, not by slow, gradual variation, as held by Darwin and Wallace, but by sudden *saltations*, or sport-like mutations. According to this theory, two fundamentally distinct phenomena have hitherto been confounded under the term variation. In other words, variation, as used by

[1] A name introduced by Wilhelm Haacke (*Gestaltung und Vererbung*, p. 31).

Darwin and others, covers two classes of phenomena, totally distinct in nature, action, and effect. Variation proper is defined as the ordinary, fluctuating, or individual variation, and this is held to be absolutely impotent to form new species.

It is claimed that no amount of either natural or artificial selection can by any possibility lead this variation up to the birth of a new species. The utmost that could be attained would be an improved race that would inevitably revert to the original state as soon as left to itself.

Mutation, on the other hand, never advances by slow and minute modifications, which are continuous and cumulative, but by single, sudden jumps. In the words of De Vries: "Species have not arisen through gradual selection, continued for hundreds or thousands of years, but by jumps (*stufenweise*) through sudden, though small, transformations. In contrast with variations which are changes advancing in a *linear direction*, the transformations to be called mutations diverge in *new directions*. They take place, then, so far as experience goes, without definite direction." (Vol. I, p. 150.)

The new species arises from the old, but without any visible preparatory steps, and without intermediate connecting stages. Like the old, it is subject to variation, but as a type, it is essentially immutable.

De Vries does not deny that variation produces what may appear to be transitional forms, but he maintains that these forms in reality have no such meaning. They are to be regarded as phenomena of "transgressive variability," which may obscure, but not obliterate the specific limits.

"For," says De Vries, "the transitions do not appear before the new species, at most only simultaneously with this, and generally only after this is already in existence. The transitions are therefore no intermediates or preparations for the appearance of the new forms. The origin takes place, not through them, but wholly independently of them." (Vol. I, p. 362.)

Granting that the position with respect to the mutants obtained from the evening primrose (*Œnothera Lamarckiana*) is unassailable, does it follow that *all* new species have arisen by mutation, and that continuous variation has never had, and never can have, anything to do with the origin of species?

Plausible as is the argument and impressive as is the array of evidence presented, I can but feel that there are reasons which compel us to suspend judgment for a while on this pivotal point of the mutation theory. America is the original home of the evening primroses, and it is here that the natural history of the group remains to be worked out in the light of the experimental results obtained in Holland.

What does it mean that a few mutants keep on reappearing year after year, and that even the mutants themselves mutate, not in new lines, but in the same old ones? Persuaded as deeply as I am that we can never draw from a species anything for which no ancestral foundations preëxist, I anticipate that our wild evening primroses have revelations to make.

Whatever revelations may await future investigation in this field, the work done in the Primrose Garden of Amsterdam will stand as a classical contribution to the new biology, and as one of the very best models in method of research that we have yet seen.

Natural selection, orthogenesis, and mutation appear to present fundamental contradictions; but I believe that each stands for truth, and that reconciliation is not distant.

The so-called mutations of *Ænothera* are indubitable facts; but two leading questions remain to be answered. First, are these mutations, now appearing, as is claimed, independently of variation, nevertheless the products of variations that took place at an earlier period in the history of these plants? Secondly, if species can spring into existence at a single leap, without the assistance of cumulative variations, may they not also originate with such assistance? That variation does issue in new species, and that natural selection is a factor, though not the only factor, in determining results, is, in my opinion, as certain as that grass grows, although we cannot see it grow.

Furthermore, I believe I have found indubitable evidence of species-forming variation advancing in a definite direction (orthogenesis), and likewise of variations in various directions (amphigenesis). If I am not mistaken in this, the reconciliation for natural selection and orthogenesis is at hand.

I am aware that orthogenesis is held by many to be utterly incompatible with both natural selection and mutation. "The Darwinian principle demands," says De Vries, "that species-forming variability and mutability *be indeterminate in direction.* Deviation in all senses must arise, without favor to any particular direction, and especially without partiality for the direction proceeding from the theory to be explained. Every hypothesis which departs from this principle must be rejected as teleological, and therefore unscientific." (Vol. I, p. 140.)

Again (p. 180) the same point is amplified: "Again and again, and by authors of different aims, it has been insisted upon that species-forming variability must be *orderless.* The assumption of a *definite variation-tendency* which would condition, or even favor, the appearance of adaptive modifications, lies outside the pale of the natural science of to-day. In fact, the great advantage of Darwin's doctrine of selection lies in this, that it strives to explain the whole evolution of the animal and plant kingdoms without the aid of supernatural presuppositions. According to this doctrine, species-forming variability goes on without regard to the qualification of the new species for maintaining themselves in life. It simply supplies the struggle for existence with the material for natural selection. Whether this selection takes place between individuals, as Darwin and Wallace supposed, or decides between whole species, as the mutation-theory demands, ultimately it is, in either case, simply the ability for existence under given external conditions that decides upon the permanence of the new form" (p. 180).

I take exception here only to the implication that a definite variation-tendency must be considered to be teleological because it is not "orderless." I venture to assert that variation is *sometimes* orderly, and at other times rather disorderly, and that the one is just as free from teleology as the other. In our aversion to the old teleology, so effectually banished from science by Darwin, we should not forget that the world is full of order, the organic no less than the inorganic. Indeed, what is the whole development of an organism if not strictly and marvelously orderly? Is not every stage, from the primordial germ onward, and the whole sequence of stages, rigidly orthogenetic? If variations are deviations in the directions of the developmental processes, what wonder is there if in some directions there is less resistance to variation than in others? What wonder if the organism is so balanced as to permit of both unifarious and multifarious variations? If a developmental process may run on throughout life (*e. g.*, the lifelong multiplication of the surface-pores of the lateral-line system in Amia), what wonder if we find a whole species gravitating slowly in one or a few directions? And if we find large groups of species all affected by a like variation, moving in the same general direction, are we compelled to regard such "a definite variation-tendency" as teleological, and hence out of the pale of science? If a *designer* sets limits to variation in order to reach a definite end, the direction of events is teleological; but if organization and the laws of development exclude some lines of variation and favor others, there is certainly nothing supernatural in this, and nothing which is incompatible with natural selection. Natural selection may enter at any stage of orthogenetic variation, preserve and modify in various directions the results over which it may have had no previous control.

It has always appeared to be one of the greatest difficulties for natural selection to account for the incipient stages of useful organs. Orthogenesis, as I hope to make clear, removes this difficulty from a large portion of the field.

It should be noted in this connection that the difficulty of incipient stages is not what it is so generally presumed to be. The advocates of natural selection habitually assume that the evolution of an organ or character begins with an "infinitesimal rudiment," which has no way of emerging from its functionless state except through minute chance variations in various directions. In this assumption the problem is misconceived. The characters we meet with to-day have rarely, if ever, arisen by direct evolution from useless rudiments. When we know enough about a character to undertake to trace its genesis, the "rudiment" imagined to lie so near recedes, and we are led on, not to a "beginning," but to an antecedent; and if we are fortunate enough to be able to advance farther, we come to another antecedent, and so on. The series of antecedents stretches ever as far as we can see. As we repeat this experience with different characters, looking always for the primordial rudiment, our childish faith in such "beginnings" gives way to the conviction that the chase is led by a phantom.

No one of our sense-organs, for example, can be traced to a rudiment, except in the embryological sense. The eye of the vertebrate may appear as a rudiment in the embryo, but no one can doubt that it has had a phylogenetic history, the first term of which — if first there be — must have been very different from its present embryonic rudiment. To assume that the eye began in some indifferent variation that fluctuated or mutated, chance-wise, into a state of incipient utility, and was then developed in a direct line to its present stage of complex adaptations, either gradually or *per saltus*, would be hardly more satisfactory than appealing to a miraculous succession of miracles. It is impossible to believe that such a system of harmonious coadaptations could ever arise by mutation; [1] and selection, although playing a very important part in such achievements, is probably never equal to the whole task. Without the assistance of some factor having more continuous directive efficiency, selection would fail to bring out of the chaos of chance variation, or kaleidoscopic mutation, such progressive evolution as the organic world reveals.

In order to show that such a factor is essential, and that it is actually present, supplying the indispensable initial stages, and holding the master hand in the *general* direction of evolution, demonstrative evidence is, of course, required. Such evidence lies in *the history of specific characters*. But how shall we approach such a task, if no near-by rudiment is to be found as a starting-point? Rudiments and premutations are alike illusory in this regard, for their beginning is always and necessarily assumed to lie in the realm of the invisible and unknowable. If we are to keep always on ground that is open to

[1] Darwin frequently emphasized the same objection. In a letter to Asa Gray, referring to the orchids, he remarks: "It is impossible to imagine so many coadaptations being formed, all by a chance blow."

Weismann has shown in a masterly manner how inadequate is the mutation theory to account for such phenomena.

investigation, we must find our starting-points in known stages. As the laws of nature are constant, it is not essential to trace entire histories. If some chapters are sufficiently open to observation and experiment to permit of close study, we may hope, in some of the more favorable cases, to read the phenomena in their natural order, and to learn from what goes on in one part of the history the factors that govern in all parts.

The study of the problem of the origin of species resolves itself, therefore, ever more clearly into exhaustive studies of single favorable characters, in the more accessible portions of their history.

For decisive evidence we must have characters of a comparatively simple nature, the evolutional records of which, in every case, are to be read in a considerable number of different species of known common origin.

It is a great mistake to resort exclusively to domestic races, for here the ancestry contains so many unknown elements that it is often impossible to refer phenomena to their proper sources. Even the so-called "pure breeds" are decidedly impure as compared with pure wild species. The ideal situation, as regards material, is to have pure wild species in abundance as the chief reliance, and allied domestic races for subsidiary purposes.

The pigeon amply fulfills all these prerequisites. A simple and convenient character, presenting divergent courses of evolution in some species and parallel courses in others, is to be found in the wing-bars and their homologues.

It is to some chapters in the history of this character that we may now turn for evidence that natural selection waits for opportunities, to be supplied, not by multifarious variation or orderless mutation, but by continuous evolutional processes advancing in definite directions.

The rock pigeons (*Columba livia*) present two very distinct color-patterns; one of which consists of black checkers uniformly distributed to the feathers of the wing and the back, the other of two black wing-bars on a slate-gray ground. These two patterns may be seen in almost any flock of domestic pigeons.

The inquiry as to the origin of these patterns involves the main problem of the origin of species, for the general principles that account for one character must hold for others, and so for the species as a whole. Darwin raised the same question, but did not pursue it beyond the point of trying to determine which pattern was to be considered original and how the derivation of the other was to be understood. Darwin's explanation was so simple and captivating that naturalists generally accepted it as final. It is but fair to state that Darwin's conclusions did not rest on a comparative study of the color-patterns displayed in the many wild species of pigeons. Accepting the view generally held by naturalists, that the rock pigeons must be regarded as the ancestors of domestic races, the question was limited to the point just stated.

It was known that the two types interbreed freely, under domestication, and it had been reported that checkered pigeons sometimes appeared as the offspring of two-barred pigeons. Moreover, Darwin discovered that the checkers were homologous with the spots composing the bars. As the main purpose was to show that variation was present to any extent required for the origin of new species, rather than to trace its course in any specific case, and as variation was supposed to be multifarious, and progress to be guided by natural selection of the "fittest," it is not strange that Darwin failed to get the direction of variation, or to realize that in *direction* is given the key to one of the fundamental laws of evolution.

As the two color-patterns are alike in having a common element, and differ chiefly in the number of elements, it was natural enough to take the smaller number as the point of departure, and to view the larger number as "an extension of these marks to other parts of the plumage." (*Animals and Plants*, vol. I, p. 225.) With the ancestral type thus determined, and a simple mode of variation pointed out, Darwin could dismiss the problem with these words: "No importance can be attached to this natural variation in the plumage."

Whence and how the two bars arose was not explained. The mode of departure assumed to account for the checkered variety would, however, suggest that the bars themselves originated in the same manner; that is, from one or two spots arising *de novo*, as chance-variations, and the gradual extension of like spots in two rows of feathers. The one or more original spots, according to the general theory, would first appear as minute rudiments, and then be gradually enlarged and intensified by the aid of natural selection, guided by their utility as recognition marks.

Such a mode of origin would presuppose a plain, uniform gray ancestor, without any spots or bars in the wings, and would raise many puzzling questions that would be beyond the reach of investigation. For example: Why two bars? Why at the posterior end of the wing? Why do the spots taper backwards to a more or less sharp point in the checkered variety, while presenting a nearly square form in typical bars? Why should they have first extended upward, or downward, and in *two* rather than any other number of rows of feathers? If two rows of feathers were favored long enough to establish the bars for ornamental or other purposes, what freak of natural selection could have then interposed to turn a long-favored, definitely directed extension into a diffuse general extension, and thus to neutralize completely the very effects it was invoked to explain?

Natural selection could not be supposed to originate or to guide the first indifferent stages of new characters. Mutation would be equally helpless, and each step would leave a gulf of discontinuity, — a miracle that nature seems to abhor.

Turning from theoretical *impasses* to the facts, let us compare the two patterns.

In the checkered pattern all the feathers are marked alike — *no regional differentiation.* In the other type we have a conspicuous local differentiation, suggesting at once a higher stage of evolution. Checkered wings are to be found which vary all the way between a uniform marking and the barred type. If we arrange a number of unequally checkered wings in a series, running from the most to the least checkered, we shall see that the pattern approaches more and more nearly to that of two bars, as the checkers diminish in size and number. We shall notice that the pigment is reduced more rapidly in the anterior than in the posterior part of the wing.

As checkers are reduced, they gradually lose their sharp ends, and approximate the square or rounded form seen in the elements of the typical bars. The series shows a flowing gradation, that may be read forward or backward with equal facility. Darwin's view takes the bars as the starting-point and reads forward. Taking the checkered condition as the point of departure, the variation runs just as smoothly in the opposite direction. We here meet an ambiguity that is everywhere present in color-pattern problems — an ambiguity that is frequently overlooked with disastrous consequences. The only way to eliminate the difficulty is to take our evidence from several different sources, and when agreement is found for one direction, and disagreement for the other, the way is clear.

As an experiment, we may take one or more pairs of pure-bred, typically barred pigeons, and keep them isolated from checkered birds for several years, in order to see if the young ever advance toward the checkered type.

Another experiment should be tried for the purpose of seeing what can be done by working in just the opposite direction. In this case we take checkered birds, selecting in each generation birds with the fewer and smaller checkers, and rejecting the others, in order to see if the process of reduction can be carried to the condition of three, two, and one bar, and finally, to complete obliteration of both checkers and bars, leaving the wing a *tabula rasa* of uniform gray color.

If these experiments are continued sufficiently far, it will be found from the second experiment that a gradual reduction of pigment to the extreme conditions named can be comparatively easily effected, and that the direction of reduction will always be the same, from before backward; while, from the first experiment, it will be seen that it is hopeless to try to advance in the opposite direction, from the bars forward to the checkered condition. No variations will appear in that direction, but such as do appear will take the opposite direction, tending to diminish the width of the bars and to weaken their color. It is in this way that we must account for the existence of some fancy breeds in which the bars have been wholly obliterated. The direction of evolution can never be reversed.

I have tried both experiments for eight years, and as both tell the same story as to the direction of variation, I am satisfied that further experiments will not essentially modify the results.

With reduction traveling from before backward, in the manner described, we get the bars in their typical number, form, and position, as *one of the necessary stages* of the process, and without appealing to *de novo* origin, incipient rudiments, etc.

But if bars originated in such simple fashion, — *the direction of evolution being precisely the same as that of embryological development,* — if the theory of rudiments must be abandoned in this case, do we not meet the same theory again in any attempt to account for the checkers?

What kind of rudiments could be imagined? We might assume that minute flecks of pigment first appeared, one in each feather; and then, further, imagine that these purely chance originations happened to have some slight utility, and that natural selection did the rest. But it is just as difficult to account for a small as a large origin *de novo,* and the smaller it is, the more unfortunate it is for the theory of natural selection.

If we seek refuge in the doctrine of mutation, are we better off? Mutation hides itself in the undiscoverable premutation, and so we have all the difficulty of an incipient stage, and no means of advancing by ordinary variation.

Fortunately we are not driven to either alternative, for the checkers arise neither as mutations nor as rudiments, but by direct and gradual modification of an earlier ancestral mark, which came with the birth of the pigeon phylum, as a heritage from still more distant avian ancestors.

This ancestral mark is a *dark spot* filling the whole central part of the feather, leaving only a narrow distal edge of a lighter color. This mark is still well preserved in some of the old-world turtle-doves — best in the Oriental turtle-dove of China and Japan. The checker of *C. livia* differs from the dark centre of *T. orientalis* only in form and in having a lateral position. Typically this spot appears in pairs, one on each side of the feather. The two spots represent the two halves of the old central spot, which becomes more or less deeply divided by the disappearance of pigment along the shaft of the feather. This change begins at the tip of the feather and advances inward, but usually more rapidly along the shaft than at the sides, thus resulting in two checkers with more or less pointed tips.

The direction of change again coincides with that of embryonic development, the tip of the feather, where it begins, being first in order of development.

In many checkered rock pigeons we may find in the dorsal (inner) feathers of the bars *undivided* central spots, which pass gradually into the typical checkers as we pass towards the lower (outer) ends of the bars. Transitional stages of various degrees thus connect the derived with the ancestral type in *one and the same individual*, and so demonstrate that the two specific marks are not separated by impassable mutation gaps.

While it is not necessary to go beyond the wild rock pigeons and the multitude of domestic races descended from them to learn that nature has here pursued *one chief direction of color variation*, always leaving an open door, however, to minor modifications and improvements through natural and artificial selection, it is, nevertheless, highly instructive to make a comparative study of the whole group of wild pigeons, in both adult and juvenal stages. It is in this field that we find the same lessons amplified and repeated in multitudinous ways, confirmation confirmed, convergence of testimony complete.

It will be sufficient here to cite a few examples.

In the little ground doves (*Chamæpelia passerina*) of Florida, Arizona, California, Central and South America, and the West Indies, we find the turtle-dove pattern preserved in the whole breast region and in the anterior, smaller coverts of the wings, while in the posterior portion of the wings we meet with lateral spots or checkers, of higher finish than in the rock pigeons. In many coverts of the wing, we find the dark centres more or less reduced, with the distal ends of their remnants in various stages of conversion into lateral spots. Here again we find most striking proof of gradual change from one specific type to another.

In the brilliant bronze-winged pigeon (*Phaps chalcoptera*) of Australia, we have still another combination type, in which iridescent checkers coexist with the original dark centres. Here the checker seems to arise by direct differentiation of a lateral portion of the dark centre, the latter still occupying the original field and forming the ground within which the checker appears as a more highly colored spot. While the dark centre does not suffer any reduction in its field, it does lose considerably in intensity of color. The metallic spots are therefore probably built up by concentration of pigment at the expense of the dark centres. As these birds make great display of their colors in the breeding season, this departure from the orthogenetic trend of development may be attributed to natural selection.

The wild passenger pigeon (*Ectopistes*) bears checkers closely resembling those of the checkered rock pigeon, in form, color, and distribution. In this species the sexes are distinctly differentiated in color; and we have for comparison three stages in an ascending series; namely, the juvenal, the adult female, and the adult male. As in so many other birds, the male makes the widest departure from original conditions; the female occupies a lower plane; the young are nearly alike in both sexes, and may be said to recapitulate ancestral conditions with less modification than is seen in the adult of either sex.

In birds taken at random, I count in the left wing and scapulars 90 checkers in a juvenal, 51 in an adult female, and 25 in an adult male. This is pretty conclusive evidence that checkers are, or have been, disappearing in the species. Not only the number, but also the size of the checkers has been reduced. In the female the checkers are for the most part two or more times as large as in the male. The reduction in both respects has been greater in the anterior than in the posterior half of the wing, and greater along the lower edge than in the middle and back regions.

In this species we may recognize at first sight the homologues of the rock pigeon bars. On the secondaries of the female we find the homologue of the posterior bar, and on the first row of long coverts the homologue of the anterior bar. The latter is scarcely recognizable as a bar; for we see only five or six checkers in the upper half of the row, the lower half being without checkers. Nevertheless, this row represents, so far as it goes, the elements of a bar, which is already too far gone to have even a chance to attain the finish of a perfect bar.[1]

On the secondaries the checkers fall into juxtaposition, forming a continuous bar, with an irregular posterior outline, which indicates that the checkers have been unevenly reduced from behind. It is a rudely finished bar, which has sunk below the horizon of utility, if it was ever above it, and is now facing ultimate effacement. The reduction has advanced further in the male, with no improvement towards regularity of outline. Here it becomes quite certain that effacement advances from all sides, leaving but a small remnant of a bar confined to two or three feathers.

Glancing at the wing as a whole, in both young and old, it is plain that the process of obliteration is in progress over the entire checkered area. The elongated, sharp-pointed marks of the earlier pattern have rounded tips in the adult; the posterior bar is roughly emarginated; the number of checkers is reduced by a half or more; and some of the remaining ones are but little more than mere dots. It is also

[1] In the young, the checkers of this row are more numerous and much more sharply pointed at the ends. In both respects the juvenal pattern approaches more nearly a condition of general uniformity.

equally manifest that the process of reduction is making more rapid progress in the fore part of the wing and along its lower edge than elsewhere. There can be no mistake here as to the direction in which the phenomena are to be read. The direction is as certain as that the adult male stands in advance of the adult female, and still more in advance of the young bird. The significance of the case lies mainly in the fact that it is not an isolated or exceptional one. Many other species tell more or less perfectly the same story.

A parallel case, only carried still farther in the same direction, is found in the mourning dove (*Zenaidura*). The adult male and female differ but slightly, each having only about a dozen checkers visible on each side. These are confined to the scapulars, and to a few feathers at the posterior upper edge of the wing. In the young, they are more numerous, but less so than in the young passenger pigeon. The middle and fore parts of the wing in the adult have no visible checkers, but a few concealed ones which may be seen on lifting the overlying feathers. These concealed checkers, and other differences between old and young, show that the species had its origin in a checkered stock, and that its history has been analogous to that of the passenger pigeon.

The white-winged pigeon (*Melopelia leucoptera*) is a most instructive form. Although a much more highly accomplished bird in the arts of display of form, feathers, and voice, than the mourning dove, it has suffered a complete effacement of the checkers it once possessed in common with other members of the family. Indubitable proof of this is to be seen in the juvenal feathers, which, in some cases, exhibit a few pale vestigial spots in the last two rows of long coverts, at points where the checkers are usually best developed in checkered species. Another striking proof is to be found in the coverts and scapulars of the adult bird, where we find, on lifting the feathers, distinctly outlined areas, corresponding in shape and position with reduced checkers, but from which the black pigment has disappeared. These vestigial outlines, structurally defined, were first noticed in a female bird of a dark shade.[1] The outlines were more perfect than in lighter birds obtained from Arizona and California.

Similar vestiges are present in the mourning dove, and here their identification as marks formerly filled out with black pigment is freed from every shadow of doubt by checkers in all stages of obliteration.

The large wood pigeon (*C. palumbus*) of Europe has departed still more widely from the turtle-dove type, having lost all its black spots except a few in the neck patches, which have retreated so far from the tips of the feathers as to be concealed. The gray plumage

[1] Captured in Jamaica by Dr. Humphreys.

and the white streak along the edge of the wing mark a plane in the evolution of this bird very nearly identical with that of the white-winged pigeon. A little higher plane has been reached by our band-tailed pigeon of the Pacific coast, which is also a species of turtle-dove derivation, as shown in the neck-marking and in the voice and behavior.[1]

These illustrations, which could be extended into the hundreds, may be concluded with two cases, representing wide extremes, yet governed by the same law of progressive orthogenetic variation.

The crested pigeon of Australia (*Ocyphaps lophotes*) stands at one extreme, at the uppermost limit in the number of bands and in the perfection of finish. There are eleven, or at most twelve, parallel bands crossing the wing and scapulars transversely, each band marking a single row of feathers, with the regularity of zebra stripes. The width of these bands increases from before backward, beginning with a width of about ½ mm. and reaching 4 to 5 mm. on the tenth band. The eleventh band, located on the long coverts, is especially interesting, as it begins above with narrow elements, like the preceding, but is continued, from the third or fourth feather onward, by elongated *checker-like spots.*

This band, or bar, is the homologue of the anterior bar in the rock pigeon, and furnishes a standing picture of transitional continuity from one character to another, and at the same time settles beyond dispute the direction variation has pursued. So clear and decisive is the case, that one might safely predict that this entire bar is destined to be reduced to the narrow band-type seen in the fore part of the wing. We have only to turn to a closely allied species, the white-breasted crested pigeon (*Lophophaps leucogaster*) [2] to find that it has already realized the prediction to the full, having every checker in this row converted into a typical band-element.

Moreover, the transformation has already begun in the first feather of the next and last row, so that the same prediction could be extended to this bar, which is the homologue of the posterior bar in the rock pigeon.

Glancing again at Ocyphaps, and looking at the wing as a whole, the course of transformation, its mode, direction, and future termination are all very clearly defined. The wing-pattern, as shown especially in the light edges of the juvenal plumage, takes us clear back to the turtle-dove type. Next came the checkered pattern similar to that of the primitive rock pigeon. Reduction of pigment, proceeding from before backward, fashioned the bilateral checkers from the uni-central spots. The reduction kept on in the same

[1] Minute blotches of black were found in the longer scapulars of a few individuals. These are probably atavistic reminiscences of lost spots.

[2] This bird is comparatively rare, and I have seen but a single pair that recently came to hand through the kindness of Frank M. Chapman.

direction, shortening the checkers and transforming the rows successively into narrow bands, eventually reaching the eleventh row, where we find only one or two complete steps, followed by a graded series of 4 to 6 steps, less and less decided, until we lose every trace of them. So finely graded are these steps in some females that it is difficult to locate the vanishing-point.

Unless the process of transformation is arrested by the extinction of the species, or through the intervention of some more potent modifying influences than have thus far appeared, the fate of both posterior bars is irrevocably sealed. Granting that natural selection may be credited with strengthening the iridescent splendor of these bars, I believe that the orthogenetic influences are bound to prevail here as in the white-breasted species.

But is there any direct proof that the transformation is actually making progress to-day? May not these transitional steps go on appearing generation after generation, without ever making any permanent progress?

We have to concede that we cannot follow the processes that reveal themselves in steps. We can at most only see what is done — not the doing. We are entirely in the dark as to the time required to carry the change through a single row of feathers. But we know that this has been done in three other species of the same family. We see that after it is done, *not before,* the transitional steps appear in the next and last row. Moreover, — and this is as close as we can hope to get to actual seeing, — we find that *progress of just the kind we are looking for is certainly made in passing from the juvenal to the adult plumage.* This is an ontogenetic change of a few weeks, which we can easily demonstrate by experiment to be progressive and continuous. The corresponding phylogenetic advance has left no other record, and hence we only know that it took time — that it was not a momentary salt. In the adult plumage, *one or two full steps are taken beyond the juvenal stage, and taken precisely at the points premarked by transitional steps.* The number of transitional steps is increased at the same time.[1]

As the next and last illustration, I take a case in which the bars are verging to complete obliteration. The well-known wild stock dove (*C. œnas*) of Europe may serve as a convenient and instruct-

[1] One point here should not escape attention; namely, that the transitional steps in Ocyphaps form a *linear* series; but there is nothing artificial or arbitrary about it. It is a small-number series, each element of which stands in an appointed place, and marks the height to which the transformation process rose at that point in its course. Such a series cannot be open to the objections which De Vries has very justly made against large-number series, the elements of which are collected at random and then arranged arbitrarily to display transitional continuity.

In the Ocyphaps series there is some fluctuation, the series varying in length, but always advancing in one predetermined direction, like a tidal flow guided along a prepared channel, and flowing to varying distances, according to the initial momentum.

ive example. In this pigeon we find that reduction of the checkers has swept over the whole wing, leaving nothing except a few obsolete spots, which we recognize as vanishing elements of bars formerly more highly developed, and homologous with those of the rock pigeon.

Here we find what at first glance looks like extraordinary variability, suggesting mutations, incipient stages, bars *in statu nascendi*, etc. The selectionist and the mutationist could each find what he looks for. The first thing to decide is the *direction* in which the phenomena are to be read. Is it a positive, progressive upbuilding of new characters, or a negative, retrogressive weakening of old characters? I have already anticipated the answer, and will now briefly show how the direction of variation is decisively settled.

(1) These spots have every outward appearance of being reduced remnants, such as we get in passing from the checkered to the barred condition in rock pigeons. They are rounded or squarish in form, frequently irregular and thin at the edges, dull in color as if fading, etc.

(2) The smallest stages are not found on the exposed surface of the feathers, but lie *concealed* beneath the overlapping feathers next above or in front. Concealed spots admit of but one interpretation. This pigeon is a not distant relative of the rock pigeon, has a similar gray ground, and is therefore probably moving in a parallel direction, only more advanced.

(3) The spots are found at the posterior end of the wing, near the upper edge, on one to three tertials and on a few long coverts. In some cases they occur also on a few of the second row of long coverts, but here they are always very small and completely concealed. They are thus in the position occupied by vanishing spots generally.

(4) The adult plumage makes no advance in the number of spots, and some spots (second row of long coverts) visible in the young, are completely concealed in the adult. This indicates degeneration unmistakably.

(5) The stock dove, although sometimes having a concealed third bar of few spots, never appears in checkered dress. It seems to have moved so far in the opposite direction that no reversal of course is now open to it.

Taking the checkered pattern as the earlier one, the various conditions of checkers and bars in rock pigeons, domestic races, and, indeed, in all the wild pigeons, become almost self-explanatory. We could not explain satisfactorily how just two bars could arise *de novo* in one species, three in another, twelve in another, and so on. The repetition of *de novo* origins would become ever more incredible. Making phylogeny our guide as to the starting-point, we find it comparatively easy to thread our way through the maze of patterns existing among five hundred or more species of pigeons, and even to trace affinities farther back in the bird world.

The orthogenetic process is the primary and fundamental one. In its course we find unlimited opportunities for the play of natural selection, escape the great difficulty of incipient stages, and readily understand why we find so many conditions arising and persisting without any direct help of selection.

Charles Darwin.

"As natural selection acts solely by accumulating slight, successive, favorable variations, it can produce no great or sudden modification." *Origin of Species*, ch. xiv, p. 421.

"Slight individual differences, however, suffice for the work, and are probably the sole differences which are effective in the production of new species." *Animals and Plants*, vol. II, ch. xx, p. 233.

"As modern geology has almost banished such views as the excavation of a great valley by a single diluvial wave, so will natural selection, if it be a true principle, banish the belief of the continued creation of new organic beings, *or of any great and sudden modification in their structure*." *Origin of Species*, ch. iv, p. 98.

August Weismann.

"The simultaneous modification of numerous cofunctioning parts, in essentially different ways, yet in harmonious functional relations, points conclusively to the fact that *something is still wanting to the selection of Darwin and Wallace*." *Germinal Selection*, p. 22.

"We know of only one natural principle of explanation for adaptation, that of selection." *Ibid.*, p. 61.

"The three principal stages of selection; that of *personal selection*, as held by Darwin and Wallace; that of *histonal selection*, as upheld by Wilhelm Roux in the form of a 'Struggle of the Parts;' and finally, that of *germinal selection*, the existence of which I have endeavored to establish — these are the factors that coöperate to maintain the forms of life constantly capable of life." *Ibid.*, p. 60.

"The harmony of the direction of variation with the requirements of the conditions of life is the riddle to be solved. *The degree of the adaptation which a part possesses itself determines the direction of variation of that part*." *Ibid.*, p. 54.

"*When a determinant has assumed a certain variation-direction it will follow it up of itself, and selection can do nothing more than secure it a free course by setting aside variations in other directions by means of the elimination of those that exhibit them*." *Evolution Theory*, vol. II, p. 123.

Carl von Nägeli.

"Between the *theory of selection and that of direct causation*, there is, apparently, only a little difference, since, according to the latter, the present condition of the organic world would likewise result from individual variation and elimination. But these two processes [selection and direct causation] differ fundamentally in their causal import. According to Darwin, variation is the germinating factor, selection the directing and regulating factor; according to my view, variation is at once both the germinating and the directing factor. According to Darwin, selection is indispensable; without it there could be no progression, and organisms would remain in the same condition as at the beginning.

In my opinion, competition simply removes what is less capable of existence, but it is wholly without influence in bringing to pass anything more perfect or better adapted." *Theorie der Abstammungslehre*, p. 285.

"The fortuitous or directionless variation of individuals would be conceivable, if it were conditioned by external influences (food, temperature, light, electricity, gravitation); for, as these causes obviously cannot be brought into any definite relation to the more or less complex organization, they must effect sometimes a positive, sometimes a negative, step. If, however, the causes of variation are internal, in the constitution of the substance, then the matter stands otherwise. In this case *the determinate organization of the substance must exercise a restricting influence upon its own variation ;* and this influence, as development begins at the lowest point, can only take effect in an upward direction." *Abstammungslehre*, p. 12.

"Individuals transmit to their offspring the tendency to be like themselves, but the offspring are not perfectly like the parents. *The tendency to variation must therefore also be transmitted.* A primordium, if all conditions are favorable, must be able to develop ever farther in a series of generations, as a capital enlarges to which interest is added annually; for each generation inherits from the preceding not only the possibility to realize the capital, but also the possibility to add the interest." *Individuality in Nature*, 1856.

Hugo de Vries.

"According to the theory of mutation, species have not arisen through gradual selection continued for hundreds or thousands of years, but by steps, through sudden though small transmutations. In contrast with variations, which are changes advancing in a linear direction, the transformations to be called mutations diverge in new directions. They take place, then, so far as experience goes, without definite direction, *i. e.*, in various directions." *Die Mutationstheorie*, vol. I, p. 150.

SECTION B — PLANT MORPHOLOGY

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(*Hall* 2, *September* 22, 10 *a. m.*)

CHAIRMAN: PROFESSOR WILLIAM TRELEASE, Washington University, St. Louis.
SPEAKERS: PROFESSOR FREDERICK O. BOWER, University of Glasgow.
PROFESSOR KARL F. GOEBEL, University of Munich.
SECRETARY: PROFESSOR F. E. LLOYD, Columbia University.

PLANT MORPHOLOGY

BY FREDERICK ORPEN BOWER

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THOSE who organized these congresses left to the guests whom they honored with their invitation a high degree of freedom in the handling of their subject. In the exercise of that freedom, which I gratefully acknowledge, I have decided not to attempt any general dissertation on the present position of plant morphology as a whole, but to discuss certain topics only in the morphology of plants, which at present take a prominent place in that branch of the science of botany. These centre round the question of the relation of the axis to the leaf in vascular plants.

The progress of plant morphology has shown certain well-marked phases in its history, and we stand at the moment on the threshold of a new one. First came the mere description and delineation of the mature form, with special reference to the higher flowering plants. This period included the work of the herbalists, and early systematists, and led to classification as its chief end: but it was enlivened by occasional generalizations, such as that of Wolff, who regarded all appendages of the axis as leaves. It was deeply influenced later by the poetic gloss cast over it by Goethe, in his idealistic doctrine of metamorphosis. But this, and the development of the spiral theory, led the stream of botanical thought temporarily away from fact into a region of surmisings.

From these it was strongly recalled by the initiation of the *second* phase, about the middle of the last century, the basis of which was the dictum, formulated by Schleiden, that "the history of development is the foundation for all special botanical morphology." The study of development thus introduced for the individual part was soon extended to the whole life-cycle, and especially among the lower forms, which had been so long neglected. The year 1848 should be marked with a white stone in the chronology of every morphologist, for in that year the essential outline of the life-history of a fern was completed by Suminsky. Hofmeister followed in quick succession with the enunciation of the fundamental homologies in fern and moss; and thus was laid, though upon a purely comparative basis, the foundation of a scientific morphology for vascular plants. But the comparisons were still formal, and might have been applied equally well to dead as to living things. The inspiration of the breath of life came with the theory of evolution: the facts then first "lived, and stood upon their feet." It is, however, remarkable how slowly the change of view brought by the theory of evolution permeated morphology. Sound though Hofmeister's conclusions were on the comparison of either generation as a whole, the same could not be said of the comparison of the parts. It took almost a generation after the publication of the *Origin of Species* for botanists to achieve any practical appreciation of evolution as a factor in the morphology of the appendages. The position up to 1874 is well reflected in the text-book of Sachs. Though he himself points out the limitations necessary to such a method, Sachs proceeds in the morphological section of his book on the footing that in vascular cryptogams and phanerogams "every organ is either a stem, or a leaf, or a root, or hair." Sporangia are held to be the results of metamorphosis of vegetative parts. The conception of homology which underlies such a grouping is dictated rather by convenience of definition and of classification than by any deeply lying aspiration after historical truth. An important step towards placing the morphology of the appendages upon a sounder footing was taken by Goebel in 1881, when he asserted the independence of the sporangium, as an organ *sui generis*, and not a result of metamorphosis of any vegetative part. This was upheld by Sachs in the following year, in his *Vorlesungen*.

Another feature, and perhaps the most important, of the *Vorlesungen*, was that in them Sachs for the first time gave due weight to the physiological aspect of morphology, and thus harmonized those two branches of study which had too long been kept asunder. The increasing attention thus given to physiology, and to the effects of external influences, has naturally led to the initiation of a *third* phase in the history of morphology: I mean the phase of experiment, with a view to ascertaining the effect of external agencies in determining form: that phase is still nascent, and carries with it high possibilities. But it is well in the enthusiasm of the moment to keep in view the limitations which hedge it round: it is to be remembered that the effect of external conditions upon form is always subject to hereditary control, and that thus the whole field of past history is still left open to speculation. This seems to have been forgotten by a recent writer, who remarks that "the future lies with experimental morphology, not with speculative morphology, which is already more than full-blown." Though this assertion contains an important truth, inasmuch as it accords prominence to experiment, the case is in my opinion overstated. All who follow the development of morphological science will value the results already obtained from the application of experiment to the problems of plant-form. But it is necessary at the same time to recognize that the two phases of study, the experimental and the speculative, are not antithetic to one another, but mutually dependent: the one can never supersede the other. The full problem of morphology is not merely to see how plants behave to external circumstances *now*, — and this is all that experimental morphology can ever tell us, — but to explain, in the light of their behavior now, how in the past they came to be such as we now see them. To this end the experimental morphology of to-day will serve as a guide, and as a check to the speculative branch, limiting its exuberances within the lines of physiological probability: but experiment can never replace speculation, for experiment cannot reconstruct history. It is impossible to rearrange for purposes of experiment all the conditions, such as light, moisture, temperature, and seasonal change, on the exact footing of an earlier evolutionary period: and even if this were done, are we sure that the subjects of experiment themselves are really the same? There remain the factors of hereditary character, and of competition, which cannot possibly be put back to the exact position in which they once were. There must always remain a margin of uncertainty whether a reaction observed under experiment to-day would be the exact reaction of a past age. So far, then, from experiment competing with or superseding speculation in morphology, it can only act as a potent stimulus to fresh speculation, wherever the attempt is made to elucidate the problem of descent. It will only be those who minimize the conservative influence of heredity, or, it may be, relegate questions of descent to the background of their minds, who will be satisfied by the exercise of an experimental method of morphological inquiry, apart from speculation.

It has already been remarked that, notwithstanding the soundness of Hofmeister's comparison for the alternating generations as a whole, the homologies of the parts remained unsatisfactory: the chief reason for this was that the grouping was not derived from comparison of nearly allied species; nor does it seem to have been held as important to consider critically whether such parts as were grouped together were or were not comparable as regards their descent. For long years after the publication of the *Origin of Species* homology had no evolutionary significance in the practice of plant morphology. But in the sister science of zoölogy this matter was taken up by Ray Lankester in 1870, in his paper "On the Use of the Term Homology in Modern Zoölogy, and the Distinction between Homogenetic and Homoplastic Agreements." Many botanists at the present day would be the better for a careful study of that essay. He pointed out that the term homology as then used by zoölogists belonged to the Platonic school, and involved reference to an ideal type. This meaning lay at the back of Goethe's theory of metamorphosis in plants, and it seems to have been somewhat in the same sense that homologies were traced by Hofmeister. Lankester showed that the zoölogists' use of the term "homologous" included various things: he suggested the introduction of a new word to define strict homology by descent: structures which are genetically related in so far as they have a single representative in a common ancestor, he styled "homogenous;" those which correspond in form, but are not genetically related, he termed "homoplastic."

It is important at once to recognize that the strict "homogeny" defined by Lankester as that of "structures which are genetically related in so far as they have a single representative in a common ancestor" can only be traced in the simpler cases of plant-form: it implies the repetition of individual parts, so strictly comparable in number and position as to stamp the *individual identity* of those parts in the successive generations. The right hand of a child repeats in position and qualities the right hand of the mother, and of the race at large: here is a strict homogeny. In the plant-body such individual identity of parts of successive generations is not common. It may be traced, for instance, in the cotyledons, and the first plumular leaves of seedlings of nearly related species, or in their first roots. But as a consequence of that continued embryology, which is so constant a feature in the plant-body, the number of the appendages of any individual is liable to be indefinitely increased, while often the absence of strict rule in their relative positions makes their identical comparison in different individuals impossible. This is especially clear in the case of roots of the second, and higher orders, for they do not correspond in exact number or position in seedlings. What we recognize in such cases is, then, not the individual identity: but their similarity in other respects: and when we group them under the same head we recognize, not their strict homogeny according to the definition of Lankester, but their essential correspondence, as based upon the similarity of their structure, and of their mode of origin upon and attachment to the part which bears them. This is also the case with the antheridia and archegonia of the pteridophytes, which are as a rule definite neither in number nor in arrangement, and are subject to variation in both respects, according to the conditions which may be imposed upon them by experiment: nevertheless, they accurately maintain their structural characters, and their essential correspondence is thus established, but not their individual identity. It is clear that this is a comparison of a more lax order than the recognition of their individual homogeny would be.

But if room for doubt of the strictest homogeny be found in simple cases such as these, what are we to expect from the comparisons of less strictly similar parts of the plant, such as cotyledons, scale-leaves, foliage-leaves, bracts, sepals, petals, stamens, carpels? How far are these to be held to be homogenous, or in some less strict sense homologous? Or, going still further, how are we to regard those comparisons which deal with parts of different individuals, species, genera, orders, or classes? What degree of homology is to be accorded to them? In proportion as the systematic remoteness of the plants compared increases, and the continuity of the connecting forms is less complete, so the comparisons become more and more doubtful, and the use of the term "homology" as applied to them more and more lax, until we are finally landed in the region where comparison is little better than surmise. It becomes ultimately a question how far the term "homology" is to be held as covering these more lax comparisons, which are certainly not examples of "homogeny" in Lankester's sense, and are only doubtfully correlated together on a basis of comparison of more or less allied forms.

The progress of our science should be leading towards a refinement of the use of the term "homology:" an approach must be made, however distant it may yet be, to a classification of parts on a basis of descent. But though this may be readily accepted in theory, it is still far from being adopted in the general practice of plant morphology. None the less, comparison is inevitably leading to the disintegration, on a basis of descent, of the old-accepted categories of parts: of these the most prominent, and at the same time the most debatable, is the category of leaves, and they will lend themselves best to the illustration of the matter in hand.

To those who, like myself, hold the view that the two alternating generations of the *Archegoniatæ* have had a distinct phylogenetic history, it will be clear that their parts cannot be truly comparable by descent. The leaf of the vascular plant, accordingly, will not be the correlative of the leaf of a moss. Even those who regard the sporophyte as an unsexed gametophyte will still have to show, on a basis of comparison and development, that the leaves of the two generations are of common descent. I am not aware that this has yet been done by them.

But the phylogenetic distinctness of the leaves in the sporophyte and gametophyte is not the only example of parallel foliar development; Goebel has shown with much cogency that the foliar appendages of the bryophytes are not all comparable as regards their origin: he remarks, "It is characteristic that the leaf-formation in the Liverworts has arisen independently in quite a number of series" (*Organographie*, p. 261), and has shown that they must have been produced in different ways. Here, then, is polyphyleticism in high degree, seen in the origin of those parts of the gametophyte which on grounds of descent we have already separated from the foliar appendages of the sporophyte.

Such results as these for the gametophyte lead us to inquire into the views current as to the origin of foliar differentiation in vascular plants. In discussing such questions it is to be remembered that in different stocks the foliar condition of the sporophyte as we see it may have been achieved in different ways, just as investigators have found reason to believe that it was in the gametophyte. We have no right to assume that the leaf was formed once for all in the descent of the sporophyte. But at the moment we are unprovided with any definite proof how it occurred. All the evidence on the point is necessarily indirect, since no intermediate types are known between foliar and non-foliar sporophytes. Physiological experiment has as yet nothing to say on the subject. The fossil history of the origin of the foliar state in the neutral generation is lost, for the foliar character antedated the earliest known fossil-sporophytes. There remain the facts of development of the individual, and comparison, while anatomical detail may have some bearing also on the question: but all of these, as indirect lines of evidence, fall short of demonstration, and accordingly it is impossible to come at present to any decision on the point. For the purposes of this discussion, however, we shall proceed on the supposition that all leaves of the sporophyte generation originated in essentially the same way, though not necessarily along the same phyletic line.

There are at least three alternatives possible for the origin of the foliar differentiation of the shoot, in any progressive line of evolution of vascular sporophytes: (1) that the prototype of the leaf was of prior existence, the axis being a part which gradually asserted itself as a basis for the insertion of these appendages: the leaf in such a case would be from the first the predominant part in the construction of the shoot; (2) that the axis and leaf are the result of differentiation of an indifferent branch-system, of which the limbs were originally all alike; in this case neither leaf nor axis would predominate from the first; (3) that the axis preëxisted, and the foliar appendages arose as outgrowths upon it: in this case the axis would be from the first the predominant part.

The first of the above alternatives, viz., that the prototype of the leaf existed from the first, and was in fact the predominant part in the initial composition of the shoot, has been held by certain writers as the basis of origin of the leafy shoot in vascular plants.[1] On this view not only is the whole shoot regarded as being mainly composed of leaves, but some even contend that the axis has no real existence as a part distinct from the leaf-bases.[2] The way in which this is pictured as having come about is by branching of a sporogonium of a bryophyte: the sporogonial head of one limb of such a branching became vegetative as the first leaf, while the other continued its growth, and branched again: thus the apex of the first lateral appendage was of the nature of a sporogonial head: this condition has been compared with that seen in the embryo of a fern, or of some monocotyledons.[3]

This view in its general form represented the plant as constructed on a plan somewhat similar to that of a complex zoöphyte. It has more recently culminated in the writings of Celakovsky and Delpino. The former in his theory of shoot-segments (*Sprossgliedlehre*) starts from the position that the plant is composed of morphological individuals: the cell, the shoot, and the plant-stock are recognized as such. The stock is composed of shoots, and the shoot of cells. Braun recognized the shoot as the individual *par excellence:* between the cell and the shoot is a great gulf, which has not yet been filled: "between the cell and the bud (shoot) there must be intermediate steps, the limitation of which no one has succeeded in defining:" the long-sought-for individual middle step is the shoot-segment (*Sprossglied*), which is neither leaf only, nor stem-segment only, but the leaf together with its stem-segment. Now this appears to me to be purely Platonic morphology: the intermediate step *must* occur; we will therefore discover and define it. The definition of it consists in the drawing of certain transverse and longitudinal lines partitioning the shoot, lines which in the sporophyte have no existence in nature: the assumed necessity of partitioning the shoot into parts of an intermediate category between the whole shoot and the cell brings these assumed limits into existence.

In support of his theory of shoot-segmentation, Celakovsky (*loc cit.* p. 101) adduced evidence from the development of the embryos of certain monocotyledons; from certain inflorescences; from the origin of the leafy moss stem on the protonema; and from the actual existence of the leaf-forming segments in mosses and pterido-

[1] Goethe, *Die Metamorphose der Pflanzen*. Gaudichaud, *Mémoire de l'Académie de Science*, 1841. Kienitz Gerloff, *Botanische Zeitung*, 1875, p. 55. Celakovsky, *Unters. über die Homologien, Pringsh. Jahrbuch*, XIV, p. 321, 1884. *Botanische Zeitung*, 1901, Heft V, VI.

[2] Delpino, *Teoria generale della Filotassi*. For reference see *Bot. Jahresbr.*, VIII (1880), p. 118, also vol. XI (1883), p. 550.

[3] Celakovsky, *loc. cit.* Kienitz Gerloff, *loc. cit.*, compared the first leaf with half of the sporogonial head, in the case primarily of fern embryos.

phytes. But objection may be taken to all these lines of evidence. We should hardly look to either the embryos of seed-plants nor to their inflorescences for safe guidance as to the origin of the fundamental characters of shoot-construction, for both are probably highly specialized forms of shoot. Particularly would this seem to be the case in the embryo, which is nursed with a supply of endosperm within the seed, a condition far removed from what can possibly be conceived as that of a primitive leafy shoot. Moreover, the fact that certain monocotyledon embryos conform externally to such a theoretical description as is given is not sufficiently cogent in the absence of internal limits of demarkation of the constituent shoot-segments.

The details of comparison of the moss-plant and protonema are quite beside our question, which relates to vascular plants: however interesting the analogies may be between the alternating generations, they cannot rank as evidence in such a question as this: for it is quite conceivable that a perfect system of shoot-segmentation might rule in the one generation, while the leafy development in the other, having originated by a distinct evolutionary sequence, might show a quite distinct relation of leaf to axis.

The last line of evidence is from segmentation at the apex of the shoot in pteridophytes: if one cell-segment regularly produced one leaf-bearing shoot-segment, this might be held to be valid evidence of Celakovsky's view. But this argument does not apply consistently, as indeed Celakovsky himself admits. It is true that a leaf may be produced from each apical segment in some ferns: but in dorsiventral ferns, and hydropterids, leaves are not produced from the ventral rows (Klein, *Bot. Zeit.*, 1884). In *Azolla* and *Salvinia* leafless internodes intervene between successive nodes: thus there is no constant relation in ferns between apical segmentation and leaf-production. Treub's investigations resulted in his statement that "there cannot be any constant relation between the leaves and the segments of the apical cells in *Selaginella Martensii.*" Lastly, in *Equisetum*, notwithstanding the regular segmentation of the tetrahedral apical cell, the leaves show no regular relation to the segments in number or position, varying in number from three to about forty. Thus the argument from apical segmentation even in pteridophytes does not give consistent support to a theory of shoot-segmentation, while such evidence is entirely wanting in the vast majority of phanerogamic plants. Notwithstanding the ingenuity of the theory as put forward by Celakovsky, in the absence of any structural indication of the limits of the shoot-segments in the vast majority of cases, the theory does not appear to me to be sufficiently upheld by the facts.

An extreme, and indeed, a paradoxical position has been taken upon this phytonic question by Delpino. As a consequence of his studies on phyllotaxis he concluded that the axis is simply composed of the fusion of the leaf-bases: that the leaves are not appendicular organs, but central organs: that an axis or stem-system does not exist, and accordingly that the higher plants are not cormophytes at all, but phyllophytes. There will, I think, be few who will adopt this fantastic view of the shoot.

The second view, that the axis and leaf are the result of differentiation of an indifferent branch-system, of which the limbs were originally all alike, has lately been brought into prominence by Potonié.[1] Taking his initiative from the branching of the leaves in early fossil ferns, he recognizes the frequent occurrence of overtopping (*Uebergipfelung*), that is, the gradual process of assertion of certain limbs of a branch-system over others: in the branching of fucoids he finds an analogy for his observations on fern-leaves, and draws the following conclusion: that "the leaves of the higher plants have been derived in the course of generations from parts of an Algal thallus like that of *Fucus*, or at least from Alga-like plants, by means of the overtopping of dichotomous branches, and the development as leaves of the branches, which thus became lateral." Dr. Hallier, who adopts Potonié's position, prefers to draw the comparison with liverworts, which show a similar sympodial development of a dichotomous branch-system.[2]

It seems not improbable that the condition of many branched fern-leaves may have been derived through a process of "overtopping" in an indifferent branch-system of the leaf itself. But it lies with Potonié to show, on a basis of comparison of forms more nearly related to them than the fucoids, that the relation of axis to leaf in the ferns was so derived: and further, that such an origin is in any way applicable to other foliar developments in vascular plants, especially pteridophytes, such as the lycopods, equiseta, and sphenophylls. I am not aware that this has yet been done. But granting that this can be done, the question still remains whether similarity of method of branching is any criterion of comparison as to descent? And especially whether such comparison is valid between widely distinct groups, or between the different generations of an antithetic alternation? It is true that Potonié prefers to regard such generations as homologous, as is indeed essential for his view: but that does not prevent others from differing from him, or even considering the fact that the parts compared belong to different generations as fatal to his theory. For my own part I am not prepared to give up the broad conclusions as to antithetic alternation on so

[1] *Lehrbuch der Pflanzenpalæontologie*, pp. 156–159. Also *Ein Blick in die Geschichte der Bot. Morph. und der Pericaulomtheorie*, 1903, p. 33, etc.

[2] *Beiträge zur Morphogenie der Sporophylle und des Trophophylls. Morph. d. Sporophylle u. d. Trophophylls*, Hamburg, 1902.

slender a ground as similarity of method of branching represented in them both.

For sympodial development of a dichotomous system (and this is all that such "overtopping" actually is) has occurred in cases where it cannot be held to have resulted in a branching which is foliar: and of this instances can be found without going so far afield as the *Fucaceæ*. It has been shown by Bruchmann[1] that the first branching of *Selaginella spinulosa* is dichotomous, and that this is probably so for all species of the genus. This mode of branching may be repeated, but the later branches may lead by most gradual transitions to the monopodial type. Yet no one would hold that the shoots thus laterally placed are consequently foliar in their nature. Again, in *Lycopodium* the branches of successive dichotomies often develop unequally: a conspicuous example is seen in *L. unilaterale*, R. Br., where one limb develops as a strobilus, and is pushed to one side by its stronger vegetative brother. A similar unequal development of dichotomous branches probably leads to such dendroid forms as *L. cernuum*. Progressions from the dichotomous to the monopodial branching are also to be seen in the case of the roots of *Selaginella*. Such examples show that in pteridophytes progressions are found from the regular dichotomous branching to its sympodial, or even its monopodial development, in cases where it is impossible to rank as leaves those parts which are forced to assume the lateral position. This shows that such progressions are a widespread phenomenon, occurring in parts of various category. If this be so, then little value need be attached to the comparison of such branchings in plants not nearly allied to one another; these may be held to be quite distinct examples of a general phenomenon, without the one being in any sense the prototype of the other. Such reflections as these indicate that the comparison in mode of branching between the leaves of ferns and the thallus of fucoids, which forms the groundwork of the view of Potonié (or between ferns and the thalloid liverworts, as may be preferred by others), are not to be held as more than distant analogies; consequently they are no demonstration of the origin of the leaf by a process of "overtopping."

There remains the third view, which, however, is no new one: for there have not been wanting those who have assigned a more prominent place to the axis in the initial differentiation of the shoot. Perhaps the most explicit statement on this point is that by Alexander Braun, who remarks in his *Rejuvenescence in Nature* (Eng. ed. p. 107), referring to phytonic theories, that "all these attempts to compose the plant of leaves are wrecked upon the fact of the existence of the stem as an original, independent, and connected structure, the more or less distinct articulation of which certainly

[1] *Unters. u. Selaginella spinulosa*, Gotha, 1897, p. 18, etc.

depends upon the leaf-formation, but the first formation of which precedes that of the leaves." Unger also in his botanical letters to a friend (no. viii), described how "The first endeavor is directed towards the building up with cell-elements of an axis;" "those variously formed supplementary organs which are termed leaves" originate laterally upon it; and he concludes that "we may therefore say with perfect justice that the plant . . . is, as regards form, essentially a system of axes." Naegeli contemplated a somewhat similar origin of the leafy shoot, as an alternative possibility; in fact, that the apex of a sporogonium-like body elongated directly into that of the leafy stem: in which case the axis would be the persistent and prominent part, and the leaves be from the first subsidiary and lateral appendages. In my theory of the strobilus in archegoniate plants the central idea was similar to this; it may be briefly stated thus: There seems good reason to hold that a body of radial construction, having distinction of apex and base and localized apical growth as its leading characters, existed prior to the development of lateral appendages in the sporophyte: for such a body is seen in certain bryophyte sporogonia, while the prior existence of the axis, and lateral origin of the appendages upon it, is general for normal leafy shoots. The view thus put forward is indeed the mere reading of the story of the evolution of leaves in terms of their normal individual development. I have recently shown that all pteridophyte shoots may be regarded as derivatives from the radial strobiloid type, with relatively small leaves, which would thus have come into existence.

It is natural to look to the pteridophytes for guidance as to the origin of foliar development in the sporophyte, for they are the most primitive plants with leafy sporophytes. They may be disposed according to the prevalent size of their leaves in a series, leading from microphyllous to megaphyllous types. I have lately shown that such a seriation is not according to one feature only, but that certain other characters which have been summarized as "filicineous" tend to follow with the increasing prominence of the leaf: this indicates that such seriation is a natural arrangement. Now it is possible to hold either that the large-leaved, fern-like plants were the more primitive, and the smaller-leaved derivatives from them by reduction; or conversely, that the smaller-leaved were the more primitive, and the larger-leaved derivatives from them by leaf-enlargement: other alternative opinions are also possible, such as that the leaf-origin has been divergent from some middle type, or that the leaves of vascular plants may have been of polyphyletic origin.[1] For the moment we shall leave these latter alternatives aside.

[1] The view recently advanced by Professor Lignier (*Equisetales, et Sphenophyllales, Leur origine filicinienne commune,* Bull. Soc. Linn. de Normandie, Serie 5, vol.

Much of the difference of view as to foliar origin centres round the question whether originally the leaf was relatively large, or small. Those who hold that the larger-leaved forms were the more primitive will be naturally disposed towards the view of the original preponderance of the leaf over the axis, and will favor some phytonic theory; those who hold the smaller-leaved forms to be the more primitive will probably adopt a strobiloid theory of origin of the leafy sporophyte. I propose to offer some remarks on the relative probability of these alternative views.

If large-leaved prototypes be assumed generally for vascular plants, this naturally involves a widespread reduction, since small-leaved forms are numerous now, and have been from the earliest times of which we have any record. Reduction is a ready weapon in the hands of the speculative morphologist, and it has often been used with more freedom than discretion. But reduction should never be assumed in order to meet the demands of convenience of comparison, nor as a cover for doubt. The justification of a view involving reduction must be found in its physiological probability in the case in question, and this should be backed by comparisons of form, and of anatomical structure: the conclusion should also be in accordance with the paleontological record. All suggested cases of reduction where such justification is absent should be looked upon as doubtful.

Convincing evidence of reduction of leaf-complexity in an evolutionary sequence, supported on all these grounds, has been adduced in the progression from ferns, through cycado-filicinean forms, to the cycads, and it applies with special force in the case of their sporophylls. Ferns, which are essentially shade-loving and typically zoidiogamic, or amphibious, may be understood to have given rise to the cycado-filices and cycads, which are more xerophytic, and show that essential character of land-plants, — the seed-habit. Not only is such a progression physiologically probable, but it is supported by paleontological evidence, as well as by detailed facts of anatomy, and of reproductive morphology. The case for reduction of leaf-complexity seems to be here fully made out: and somewhat similar arguments will also apply for other types of gymnosperms.

7, Caen. 1903) is analogous to that of Potonié, though differing from it in detail. It involves the ranking of the lycopod leaf as a "phylloid," the leaf of the fern as a true leaf, or "phyllome," differentiated from an indifferent system of "cauloids," on which the "phylloid" appendages had become abortive. It regards the leaves of equiseta and sphenophylls as phyllomes, reduced from the larger-leaved fern-type. The argument is chiefly based on comparisons as to branching and anatomical structure. I do not think that these grounds suffice to override the probability that the leaves of lycopods are essentially of the same nature as those of the sphenophylls, or equiseta. (Compare my *Studies*, no. v.) Professor Lignier's view further involves the acceptance of homologous alternation, while he makes no mention of the chromosome-differences of the two generations. Such difficulties do not arise if the leaves of the sphenophylls and equiseta are regarded as being in the upward rather than the downward scale of development, a view of them which would equally harmonize with the anatomical comparisons of Prof. Lignier.

The facts relating to the vascular system of the shoot have also their bearing on the question of the relative size of primitive leaves. The origin of the leaf-trace from the axial stele in conifers, and also in angiosperms, has been shown by Dr. Jeffrey to be of the type styled by him phyllosiphonic. This is specially characteristic of those plants where the leaf is essentially the dominating influence in the shoot. In this I see a probability, which their physiological position as land-growing plants would justify, that the seed-bearing plants at large were descended from a large-leaved ancestry, and had undergone reduction of leaf-complexity in their descent. But while we thus recognize a probability of widespread reduction producing relatively smaller-leaved forms, it does not follow that *all* small-leaved vascular plants originated thus: on this point the anatomical evidence is of importance, as bearing on the origin of the small-leaved strobiloid pteridophytes. Of these (putting aside the hydropterids as being a special reduction-problem in themselves), there remain the lycopodiales, the equisetales, and the sphenophyllales, which are all cladosiphonic in the terminology of Dr. Jeffrey: the question will largely turn upon the meaning of this anatomical feature. I take it to be as follows: The cladosiphonic character is the anatomical expression of the dominance of the axis in the shoot: here the leaf-trace is merely an external appendage on the stele, which is hardly disturbed by its insertion: this type is seen in certain small-leaved pteridophytes. The phyllosiphonic character, on the other hand, is the anatomical expression of the dominance of the leaf over the axis in the shoot; here the insertion of the vascular supply of the leaf profoundly disturbs the vascular arrangement in the axis; it is characteristic of certain large-leaved pteridophytes, and is seen also generally in seed-plants.

It is a fact of importance that, in the individual life, the one or the other type is usually constant; but in certain ferns the progression may be traced from the cladosiphonic in the young plant to the phyllosiphonic in the mature, thus suggesting a similar progression in descent, viz., that the large-leaved phyllosiphonic ferns were derived from a smaller-leaved cladosiphonic stock. Of the converse, viz., the progression from the phyllosiphonic to the cladosiphonic state in the individual life, I know of no example among the pteridophytes, though it is true that there is some approach to it in the *Marsileaceæ*. Thus the anatomical evidence indicates a probability that, even in large-leaved ferns, the cladosiphonic was the primitive type, but that the phyllosiphonic, once initiated, is as a rule maintained; this is shown by its persistence in the seed-plants, even where the leaf has been reduced in size.

Having thus gained a valuable side-light from anatomy, we may now return to our central question of the initial relation of leaf to axis. Of the three theories already noted, the theory of overtopping, as applied to the origin of the leaf, may in my opinion be dismissed, as it is not based upon comparison of nearly related forms, while the sympodial development of a dichotomous system, on which it is founded, is a general phenomenon of branching, neither restricted to leaves, nor to the sporophyte generation. As to the other two, the facts, whether of external form or of internal structure, seem to me to indicate this conclusion, that the strobiloid condition was primitive for certain types, such as the equisetales, lycopodiales, and sphenophyllales, that in them the leaf was from the first a minor appendage upon the dominating axis, and anatomically they have never broken away from the cladosiphonic structure, which is the internal expression of their microphyllous, strobiloid state. That the filicales and also the ophioglossales were probably derived from a microphyllous strobiloid ancestry, and achieved the phyllosiphonic structure as a consequence of leaf-enlargement, this being the derivative rather than the primitive condition; its derivation is even illustrated in the individual life of some ferns. From the filicales the phyllosiphonic structure was probably handed on to the seed-plants, and by them retained, notwithstanding the subsequent leaf-reduction which followed on their adaptation to an exposed land-habitat. Thus a strobiloid origin may be attributed to all the main types of vascular plants; it seems to me to harmonize more readily with the facts than any phytonic theory does.

A prototype, which was probably a prevalent, though perhaps not a general one for the pteridophytes, may then be sketched as an upright, radial, strobiloid structure, consisting of a predominant axis, bearing relatively small and simple appendages. On our theory the origin of those appendages in descent would be the same as it is to-day in the individual development: viz., by the outgrowth of regions of the superficial tissue of the axis to form them: the axis would preëxist in descent, as it actually does in the normal, developing shoot. The origin of these appendages may have occurred independently along divers lines of descent, and the appendages would in that case be not homogenous in the strict sense. Thus there would be no common prototype of the leaf, no morphological abstraction, or archetypic form of that part. More than one category of appendages might even be produced on the same individual shoot, differing in their function on their first appearance: such has perhaps been the case in the calamarian strobilus, where the leaf-tooth cannot be readily homologized with the sporangiophore. These suggestions will suffice to indicate how elastic a strobiloid theory is, and how its application will cover various types of construction, and even such as are shown by the most complex cones of pteridophytes.

From the comparison of living species there is good reason for thinking that all the primitive leaves in certain types, such as the lycopods, were sporophylls, and that a subsequent differentiation took place, by abortion of the sporangia: thus a sterile vegetative region became defined from a fertile upper region. It may be a question whether this origin by sterilization of sporophylls is applicable to foliage leaves at large: nevertheless analogy, not only with other vascular plants, but also with the bryophytes, suggests that a similar differentiation of a sterile from a fertile region has been a general phenomenon in the neutral generation. At first in the simpler pteridophytes these regions were essentially similar to one another in form, as is still seen to be the case in some lycopods. Later, however, the sterile and fertile regions took divergent lines of development in accordance with their difference of function. The differentiation reaches its climax in the higher flowering plants. The inflorescence, or flower, on this view, though produced later than the vegetative region in the individual life, embodies the more primitive parts, viz., those which bear the sporangia and spores; the vegetative region is in its origin mostly, if not wholly, secondary. The physiological reasonableness of this view is too obvious to need insistence. As the self-nutritive powers of the gametophyte fell off in the adaptation to the land-habit, the nutritive function was taken up by the new vegetative system thus intercalated between sexual fusion and spore-production.

This is in brief outline the strobiloid theory of the shoot in vascular plants, as arising out of the facts of antithetic alternation. It will be seen that it is essentially in harmony with the view of Braun, upheld also by Sachs, that the shoot is the real morphological unit, of which leaf and axis are correlative parts. Those who adopt it will find their position simplified in regard to another question which has recently taken afresh a prominent place in morphological discussions, viz., the theory of cortication (*Berindungstheorie*). It is held by Potonié, and a similar view was also maintained by Celakovsky, that the stem has centrally an axial nature, peripherally a leaf-nature. The primitive axis (*Urcaulom*) acquires in the course of generations, by coalescence with the basal parts of its primitive leafy appendages (*Urblätter*), a mantle, — a "Pericaulom." This is what we commonly designate the cortex, which is thus regarded as not being axile in origin, but foliar. In accordance, however, with our strobiloid theory, we may presume that, as is seen in some of the bryophytes, the simple sporophyte consisted originally of a central region, — a primitive stele, — and a peripheral region, a primitive cortex. From the latter sprang the appendages, as superficial outgrowths, just as at the present day the leaves originate upon the cortex of the axis. The cortex in such cases would be, from the first, part of the primitive axis, and the outgrowths processes from it. The primitive cortex from which the appendages sprang may remain a continuous, undifferentiated band, as it actually does appear in the vast majority of leafy sporophytes; or it may in certain cases be more or less clearly marked off into regions surrounding the insertion of the individual leaves. But in the fact that these special cases exist I see no sufficient foundation for the view that each leaf is, in shoots at large, connected with a definite area of extended leaf-base: and still less for the theory that in vascular plants the cortex originated from such coalescent leaf-bases. Our theory of the strobilus would indeed presuppose that close relation of cortex and appendage, and absence of limit between them, which is so common a feature in vascular plants: and furthermore, it will readily cover the facts where the cortex is delimited into definite areas round the leaf-bases: but it does not recognize any necessity for generalizing from such cases of special delimitation, that the cortex is foliar in its origin, in shoots of vascular plants at large. It would be more ready to suggest the converse, viz., that the leaves were cortical in their origin, as indeed they are in the ontogeny.

Discussions such as these on phytonic theory, or theory of cortication, are liable to develop into mere scholastic contests. They originated in the present case in the use of terms in an unprecise sense, and the subsequent attempt to attain precision. Both these theories have proceeded from the assumption that the "leaf" is an abstract entity, distinct from the stem. Difficulties arise when the attempt is made to carry out that distinction sharply in practice, for this is nothing less than the attempt to define precisely things which in point of fact appear neither uniform nor precise in nature. The strict definition of terms used in morphological science is doubtless in itself a desirable thing; but it must be so conducted as to harmonize with the facts of individual development, while at the same time it must not violate evolutionary probability. As a matter of fact, neither in the mature state, nor in the ontogenetic or phylogenetic development of the leaf, does the structure suggest its sharp delimitation from the axis as a general feature in the shoots of ordinary vascular plants.

My present position with regard to the phytonic theories and the theory of cortication is frankly destructive: for, in the first place, if the evidence from the gametophyte generation be discounted, the facts of segmentation in the sporophyte are of the slenderest: further, I do not think that morphological insight will be advanced by attempts to define precisely the limits of the parts of the vascular shoot; it seems more in accordance with nature to accept for vascular plants the view of Braun and of Sachs, that the shoot is the original unit. What is first urgently required, in order to decide such questions, is the correct recognition of the phyletic lines which eventuated in the various appendages as we see them. Then may follow definitions of the parts, which may or may not succeed in assigning their strict limits. When this is accomplished, a terminology may follow, which shall segregate parts which have had a separate phyletic origin. Thus an evolutionary morphology of the shoot would be built up. But it is useless to accept the thesis merely in the abstract, that the basis of morphology must be in phylogeny: the principle must also be put in practice, and be ultimately reflected in our methods, and in the definitions of our terms.

A step in this direction will be the recognition that at present the word "leaf" is loosely applied: it is, indeed, a temporary makeshift borrowed from colloquial language, and used in a descriptive rather than in a strictly scientific sense. It designates collectively objects which have, it is true, formal and functional, and even topographical features in common, but have not had the same phyletic history. There is every probability that the word "leaf" will continue to be used in this merely popular sense.

This position, with its conservative use of terms fitting awkwardly upon advancing phyletic ideas, can only be properly understood by glancing back at the history which has produced it. So long as species were regarded as the individual results of creative power, the complexity and variety of their form was relegated to the arcana of the Divine Mind, and organic nature presented the aspect of a series of isolated pictures; any similarity which these might show was to be regarded as indicative of the underlying divine plan. Now that species have been threaded together by evolutionary theory into developmental sequences, they, like the ribbon of a cynemetograph, present phyletic history to the mind with all the vividness of a living drama. While monophyletic views held the field, this seemed comparatively simple: .but the conclusions thus arrived at in plant morphology were often palpably improbable. Such difficulties, together with the substantiation of examples of parallel development on a sound comparative basis, led to the modification of monophyletic views, and opened the way for less cramped conceptions. It is now customary to contemplate the plural origin of such leading features as sexual differentiation, foliar development, heterospory, the seed-habit, as well as a host of minor characters. On such examples we base a general belief that similar structures may be arrived at by divers evolutionary routes. It is this conception of polyphyleticism that we must make clear in our descriptions, if not even in our terminology.

It will be objected that to carry through a method of designating by the same term only such parts as are shown to be of common descent would produce unwieldy results. Doubtless this is true. But in the terminology of a science it is not so much convenience as truth and clearness which should be the aim. The choice is open to us either to make the terminology strictly phyletic throughout, which would certainly be cumbrous, though it would reflect the true position; or, putting phyletic distinctions in the background, to use terms in a more or less comprehensive sense, even grouping together things which we know to have been distinct in phyletic origin. Such a comprehensive sense is conveyed by the expression "homology of organization," which, as Goebel points out, "has only to do with phylogeny in so far as it recognizes a common capacity for development derivable from undifferentiated ancestors" (*Organographie*, Eng. ed., p. 19). This is indeed a collective term for the results of parallel development; it suffers from the danger of suggesting some ideal type or pattern towards which evolution has tended.

For my own part I think it matters little what our terminology be, or what the separation of categories of parts, provided we attach clear meanings to the words we use, and select those words as naturally conveying those meanings. For instance, if we fully realize that the word "leaf" is used in a sense which is not phylogenetic, but merely descriptive of those lateral appendages on the shoot which are produced exogenously, and in acropetal order, then let it remain, ranking as an expression of "homology of organization." But the appendages thus included may for clearness be conveniently divided into "phyllomes" on the sporophyte, and "phylloids" on the gametophyte, as, indeed, I suggested some years ago. Nevertheless, these again are not phyletic unities: they include parts with distinct histories, which have already been recognized in the gametophyte, while for the sporophyte a more advanced state of the science will probably provide definitions. Meanwhile we consent to a compromise in grouping these together: but the only condition upon which this can be safely done is the clear knowledge that this is a compromise by which we secure a certain convenience of description. Moreover, the acceptance of this compromise must not be understood to grant free license to argue from one to another of the forms included, as though they were equivalents: what has resulted in one line of descent can at best only throw a side-light on what has happened in another distinct line: and in proportion as the lines involved in a comparison are more remote from one another, their comparison assumes more and more the character of a mere analogy. The danger which our compromise brings with it is that this will not be clearly kept in mind. At all hazards the strict phyletic view should underlie all present morphological discussion, notwithstanding that, for mere convenience, that view may not be clearly reflected in the classification of the parts. This makes me hope that the compromise is only a temporary concession, and that it will give way ultimately to the demands which a more detailed knowledge of descent is sure to bring.

It is well, however, in connection with discussions such as these, to impress upon the lay public that all evolutionary theories are, like other scientific theories, hypotheses incapable of complete proof. No one will appreciate this more fully than biological investigators themselves, for they are in the best position to know how insufficient the evidence actually is, and how liberal a use has to be made of the imagination in bridging over the wide gaps in the series of known forms. The details of a story thus constructed depend so largely on comparative opinion, and in so slight a degree on positive demonstration, that the history as told by competent experts in comparative morphology may vary in material features. A little more weight allowed for certain observed details, or a little less for others, will be sufficient to disturb the balance of the evidence derived from a wide area of fact, and consequently to distort the historical picture. There is in truth no finality in discussions on the genesis and progress of organic life, or in the kaleidoscopic changes of opinion, since any new fact of importance will in some degree affect the weight accorded to others, and may vary the general result. It will be objected that conclusions which are so plastic are little better than expressions of personal taste, that the study of comparative morphology is therefore calculated to dishearten its votaries, while the non-specialist public, which is compelled to take its information at second hand, will be bewildered, and will conclude that it is useless to pursue a subject which shows so little stability. But on the other hand, those who follow the progress of morphology with sympathetic care will take heart when they compare its present position with that of a generation ago; it is encouraging to think that it is little more than half a century since the history of the life-cycle of a fern was first completed. In some sixty years a vast array of kindred facts have been acquired, and a theoretic structure is being raised upon them, which, though still protean, is gradually acquiring some settled form. Never has the advance of morphological thought been more rapid than at present. The support of the facts of alternation from the unexpected quarter of minute cytology has been one of the most striking features in the recent history of our science. The discovery of spermatozoids in the cycads and *Ginkgoaceæ* has filled in a gap in the story of evolution, which all followers of Hofmeister must have felt. But in no field of morphological research has investigation been more amply rewarded than in palæophytology. The luminous facts derived from fossils are shedding fresh light on obscure problems, such as the origin of the seed-habit, and helping us to locate such difficult groups as the *Psilotaceæ* and *Equisetaceæ*. When we regard these rapid advances, and truly estimate the influence they bring to bear upon morphological theory, we must surely congratulate ourselves on being devotees to a science which is very actively alive.

But at the same time the detached cynic may find in the methods of plant-morphologists, or still more sometimes in their want of method, food for much critical remark. And if he put his finger upon one mental process which more than another has introduced discord, it would, I think, be "assumption." It may be that our science is not worse than others in this respect, but I am very sure that arguments based upon ill-founded assumption have put back the progress of morphology more than anything else in our discussions. Any one can find examples for himself in the literature: some of us in our own writings. It remains for us who tread the difficult path of morphological theory to beware lest we neglect those warnings with which its course is so plentifully strewn, for it is just as much the duty of a scientific man to avoid blurring the issues for others by faulty argument, as it is to attempt to make clear to them what he himself believes to have been obscure.

THE FUNDAMENTAL PROBLEMS OF PRESENT-DAY PLANT MORPHOLOGY [1]

BY KARL F. GOEBEL

(*Translated from the German by Professor Francis E. Lloyd, Columbia University*)

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A FEW months ago I was in Jena in order to attend the unveiling of the statue there erected to M. Schleiden. Now there is hardly any other place which has been of so much significance in the development of plant morphology as this small university town. It was there that Goethe, the originator of the term "morphology," busied himself with morphological studies, and founded the idealistic system which has influenced our thought — often unsuspectedly — till the present day. There Schleiden, in outspoken opposition to the conceptions of the idealistic morphology, gave new life to the theory of development founded by Caspar Frederick Wolff in the neighboring town of Halle in the middle of the eighteenth century, and so paved the way for the brilliant discoveries of William Hofmeister. And who does not know what meaning Jena has won as the citadel of phylogenetic morphology, first through the work of Haeckel in zoölogy and later through that of Strasburger in botany? In such a morphological atmosphere the question forces itself upon us, in what relation do the morphological questions of the present stand to those of the past? Are they still unchanged in spite of the immense increase of empirical material, and have the methods of their solution only changed? Or have the problems themselves become different?

To reply to this question is not easy, and the answer must vary with the point of view of the one who makes it. For morphology is yet far from being an exact science, the results of which force themselves upon us with the compulsion of necessity. This is due to the difficulty of the materials, a difficulty which compels us to seek for hypotheses and other subjective means of explanation. It thus comes

[1] The views set forth in this lecture are presented at length in the author's *Organography of Plants*, Jena, 1898–1901, English translation, Oxford, I, 1900; II, 1905. Concerning the historical significance of Goethe, Schleiden, Hofmeister, compare Sachs' *History of Botany*, translation, Oxford, 1890.

about that views not only concerning the goal of morphology, but also as to the way in which this goal is to be reached, are widely diverse, and my own views concerning the fundamental problems of morphology are certainly far from being approved by all morphologists.

We may, indeed, say that, apart from minor differences, there are in morphology two main trends of thought which, apparently, at least, are opposed to each other, one of which we may denominate formal, and the other causal. Causal morphology is that the aim of which is to determine the causes, in the widest sense, of form-relations; this kind of morphology is the youngest, and is far less widely diffused than the formal. To us of a later period it may seem like a remarkable pleonasm to speak of a "formal morphology." Morphology is, of course, the doctrine of form, and therefore any morphology appears to be, in the nature of the case, a formal one, and, as a matter of fact, has been, in its historical development. But in spite of this fact, this definition is historically justified, for it designates the tendency of morphology which regards form as something which stands alone for itself, and takes cognizance neither of the functions of organs nor of how they have arisen. This formal morphology arose at first out of the necessities of taxonomy.[1] There had first to be contrived a terminology for the distinction and description of single plant forms. From this function morphology soon, however, became distinct, thus constituting an independent discipline which, on its part, had done taxonomy a more important service than one might have at first expected. For while taxonomy, in order to find its way amid the maze of plant forms, had to keep in view the differential characters and the separation of single forms from each other, morphology found itself under the necessity of determining what was common to the most various forms, and was accordingly directed toward more general questions; morphology taught, as Goethe expressed it, "Die Glieder der Pflanzen im Zusammenhänge zu betrachten, und so das Ganze in der Anschauung gewissermassen zu beherrschen." It resulted in the knowledge that, when we regard plants singly, manifold as their parts appear, they may yet be referred to a few elementary forms, and further, morphological research showed that the parallelism between different plant forms could be understood most easily under the assumption which we designate the theory of descent. The establishment of the theory of descent was the result of the morphological research. This we must here especially emphasize, for it shows what significance morphology has gained in respect to our general conception of organisms. But the theory

[1] How far the trends of morphology and taxonomy have of recent years drawn apart is shown, *e. g.*, in Engler's *Syllabus of the Families of Plants*, the most recent review of the plant kingdom as a whole. For the most part, the results of developmental research remain entirely disregarded in this work.

of descent has also reacted upon morphological research, to such an extent, indeed, that it has been held that phylogenetic research is to be regarded as the sole business of morphology. Thus, for example, Scott has said:

"The object of modern morphological botany is the accurate comparison of plants, both living and extinct, with the object of tracing their real relationships with one another, and thus of ultimately constructing a genealogical tree of the vegetable kingdom. The problem is thus a purely historical one, and is perfectly distinct from any of the questions with which physiology has to do." [1]

This position is certainly justified from the standpoint of the paleontologist. For him, for whom nothing but dead material is at hand, there remains nothing else to do than to make known, through careful comparative study, the structure and relationships of those organisms whose remains are available. This is a very important business. The beautiful results of phytopaleontological research, such as have been attained during the last decade in England and France, have very materially furthered our knowledge of plant forms, and have made to live again before our eyes, in a most surprising manner, and in the finest details of their structure, types long since vanished from the surface of the earth.

But does this limitation of morphology to the comparative phylogenetic method which is imposed upon the paleontologist exist also for the morphological study of living plants?

There are many of the opinion of Scott; and, indeed, a special "phylogenetic method," which is said to be a characteristic of modern morphology, has even been talked of.[2]

Were this the case, then the only difference between the morphology of the present and the earlier, idealistic morphology would consist in this, that in the place of the general ideas with which this operates, as, *e. g.*, "type" "plan of organization," etc., there would be found phylogenetic conceptions. Such general abstractions are, however,

[1] Address to the botanical section, British Association for the Advancement of Science, Liverpool, 1896.

[2] Cf. Haeckel, *Generale Morphologie*, I, p. 50; Strasburger, *Ueber die Bedeutung phylogenetiseher Methoden für die Erforschung lebender Wesen*, Jena, 1874; also the criticism, pertinent according to my opinion, which Al. Braun made concerning the setting forth of the phylogenetic method, in his treatise, *Die Frage naeh der Gymnospermie der Cycadeen* (*Monatsber. der Berliner Akad.*, 1875). Al. Braun rightly maintained that the theory of descent did not offer a new method, but was really the result of earlier methods, and that the results of paleontology are far too fragmentary for the construction of a phylogenetic tree of the organic kingdom. This is yet true, thirty years later, after we have attained a much more exact knowledge of the organization of fossil plants through the important work of Williamson, Scott, Oliver, Renault, and others. We have found, *e. g.* that the group of cycadofilices possessed seeds. It has, however, not become possible to derive a group of living plants from the cycadofilices directly. It has become highly probable that these have sprung from fern-like ancestors; but from what form it remains at this time entirely unknown. Concerning fossil plants see the work of Scott, *Studies in Fossil Botany*.

even now difficult to escape, since we can set forth real descent-series only in the fewest instances, and, accordingly, we cannot actually point out the stem-forms. Yet Darwin himself said:

"We have seen that the members of the same class, independently of their habits of life, resemble each other in the general plan of their organization. This resemblance is often expressed by the term 'unity of type;' or by saying that the several parts and organs in the different species of the class are homologous. The whole subject is included under the general term of Morphology. This is one of the most interesting departments of natural history, and may almost be said to be its very soul." [1]

The significance of formal morphology cannot be more forcibly expressed than it was by Darwin. And yet we see that, in Germany at least, interest in morphological problems has greatly decreased. Morphological treatises have become relatively less numerous; morphological books, even such excellent ones as, *e. g.*, Eichler's *Blüthen-diagramme*, do not pass through a second edition, while anatomical and physiological works appear repeatedly in new editions; evidently meeting the demands of the botanical public more fully than morphological works.[2] This may be referred to reasons which lie partly without and partly within morphology itself; both turn out to be true. Histology, cytology, and experimental physiology have developed remarkably; new methods in this field promise new results; particular lines of work, however, such as descriptive anatomy, are especially favored because the perfection of the methods of research have quite materially lightened the task of working through a vast array of materials, especially for those to whom the other fields of botanical study are more or less unfamiliar.

But the reasons for the phenomena which lie within the field of morphology are also clear. Some parts of morphology are well worked out, as, *e. g.*, the doctrine of the more obvious form-relations of plants; and the homologies, at least in the large, are determined, although in the matter of detail much remains vague, and offers a wide field for exhaustive studies in development. More and more, however, these studies bear the stamp of repetition and complement, from which the stimulus of newness is wanting, or they are carried on upon materials which are very difficult to obtain. The constructions of the idealistic morphology, however, often proved to be untenable.

But the first experiments towards a causal morphology brought disillusion. For only a short time lived the hope of being able to

[1] *Origin of Species*, II, 142.

[2] As Eichler wrote me shortly before his death, he would have been glad to publish a second edition of his work in order to bring to light the numerous thitherto unpublished observations of Al. Braun. The publishers demurred, however, on the ground that there still remained unsold a large number of copies of the first edition. Since then the book has, it seems, gone out of print. Nor to my knowledge has any other morphological work passed through a second edition.

answer, *e. g.*, the question as to the arrangement of leaves through the effect of mechanical factors, or to refer the form-relations of a plant to the direct influences of gravity and light on the plant. It soon became evident, however, that such involved problems are not to be unraveled by such simple means, and this may well have resulted in the suppression of interest in morphology.

At this point phylogenetic morphology appeared to take on a new lease of life. This, however, in natural science is connected, on the one hand, with the appearance of a new, creative idea, and, on the other hand, with the discovery of new methods. Now the theory of descent has powerfully stimulated morphological research. But has it brought to it, as, *e. g.*, Strasburger has held, a new method, the phylogenetic? Alexander Braun has already properly answered this question in the negative.

Scott, also, has maintained that historical morphology (as regards both living and fossil plants) is dependent upon comparative study, that is, makes use of the same method as was in evidence before the appearance of the theory of descent; indeed, the most important homologies in the plant kingdom became known through Hofmeister at a time when the idea of descent was far from that general acceptation which it at first gained through the life-work of Darwin.

The method has then from first to last remained the same: the most comprehensive comparison not only of mature forms, but also their development. A special "phylogenetic method" there is not, but only a phylogenetic conception of morphological problems. These are, however, just as at first was the case with idealistic morphology, purely formal. Modern morphology in my sense, however, differs from the older in this, that it goes beyond the method of mere comparison. It allows the setting up of genetic trees to rest for the while, since, with our present knowledge, this meets with insuperable difficulties, and has brought almost as much disappointment as the idealistic morphology. For just this reason, namely, because we are persuaded that no other forces have been at work during the phylogenetic history than those which now control the development of each particular organism, do we wish, first of all, more exactly to learn what these are. We are concerned not alone with the determination of the single successive stages of development. These must, of course, be followed, but in addition we should follow all phenomena which may be got at by our means of observation, whether directly, by the microscope, or by chemical analysis. We may, therefore, say: The basal problem of the present-day morphology is not phylogenetic development, but development in general. We must, therefore, take our departure from the investigation of individual development (of ontogeny), for only this lies before us complete and without any break, and further, because the study of ontogeny only may proceed from the experimental point of view. An understanding of development is possible only when the conclusions to which the observation of the phenomena of development has led us, rest upon experimental proof; in other words, when we ask questions of nature, and obtain our answers to them.

Every little step — and with such only are we now concerned — beyond the mere descriptive consideration of development is here of significance, and brings the possibility of further progress. And small indeed, I may add, appears to be such advance to those who from the beginnings of phylogenetic morphology have, like Sisyphus, sustained their courage to roll again and again up the mountain the rock of phylogeny as often as it has rolled down.

It may now be attempted to examine somewhat more closely in certain particular examples the relation between phylogenetic and causal morphology. One of the changes which phylogenetic morphology has brought with it is that it seeks to ascertain which form is "primitive" and which derived.[1] Idealistic morphology has borne in upon us no conviction on this question, since it derives all forms from a type which is present only as a conception. But phylogenetic morphology must, on the one hand, always reckon with the possibility of polyphyletic development, and, on the other hand, it can operate not only with reversionary structures, as did the idealistic morphology, but must be far more concerned in determining which forms within the series which it proposes stand near-

[1] I do not, of course, deny that there are forms which we may designate primitive. What, however, is insisted upon in the above text is as follows:

(1) The different meanings of the word "primitive." It can mean either

(*a*) A form which stands nearer to the stem form than any other. In this sense we may designate the *Gymnospermæ*, *e. g.*, as more primitive than the *Angiospermæ*, because it may be admitted that all seed-plants are derived from heterosporous *Archegoniatæ*, while it is the *Gymnospermæ* which maintain this character most evidently.

(*b*) "Primitive" is also used often in the sense of "phylogenetically older." At this point, however, we come into the field of hypothesis, for the paleontological facts are far too few to afford us a picture of chronological series of plant groups. It is known that there are several parallel developmental series (*e. g.*, the appearance of heterospory in different groups of *Pteridophyta*). Forms which appear primitive may, then, in reality constitute the end of a very long series, younger perhaps than one which does not appear to be primitive and is derived from other stem-forms, with which then it is not genetically related. It is, *e. g.*, very easily conceivable, though at present incapable of proof, that heterospory, in so far as it is older than isospory, arose at first from spores of sexual cells (male and female swarm spores), and that from this point on the development of the spores took on a more or less marked vegetative character. Were this the case, then the isosporous *Pteridophyta* would be phylogenetically younger than the heterosporous, and the *Bryophyta* would be a parallel development to the *Pteridophyta*. This is, to be sure, only a possibility which one may at first regard as fantastic, which, however, is no more so than many other conceptions which have been put forth at one time or another.

(2) The difficulty of distinguishing with certainty between primitive and reduced forms.

est the common point of derivation. It seeks, then, with diligence after "primitive" forms. But in this search we meet with great difficulties. In the first place, we are inclined to regard those forms as primitive which have simple form-relations, and unmarked division of labor. But such forms may also have arisen by reversion, and if one looks over botanical literature, he sees, at least so far as the relationships between the larger groups are concerned, there exists no agreement as to which forms are to be regarded as primitive and which derived; opinion on this point often changes with the fashion. Thus the thallose liverworts have up till now been regarded as more primitive than the foliose, because the vegetative body of the former is much more simple in construction than that of the latter, and between them there are found gentle gradations. Recently, however, the attempt has been made to derive the thallose from the foliose forms.[1] This is not the place to examine the evidence for or against such derivation. How vacillating is the point of view from which it is judged what form is primitive is shown by the various positions which have from time to time been given to the apetalous dicotyledons.

The old morphology regarded these as reduced forms because their flowers are less fully differentiated than those of most of the other dicotyledons. Eichler has, however, already shown that there is no ground for maintaining that the corolla in the *Iuliflorœ* and *Centrospermœ* has suffered reduction; and on this point we can only agree with him. But must they, because the perianth shows simply form-relations and also because the number-relations within the flower are not always constant, be therefore primitive? Even if we admit that these groups have a great geological age, it is not proved that they stand as regards their total organization on a lower plane of development; old and primitive forms are the same only when it can be shown that the former stand nearer to the stem forms of the angiosperms than other forms. If this is not capable of proof, then the old forms may just as well be the end terms of long developmental series as others, only that the differentiation of organs has not taken place to the same degree as in the others. Now, we do not know the stem forms of the angiosperms, and they may never, perhaps, be known. But even if we content ourselves by reconstructing them on the basis of comparative study, I can find no reason, *e. g.*, to regard the *Cupuliferœ* as primitive forms, while I can find many reasons for not doing so. Here may be cited

[1] Wettstein, *Handbuch der Systematischen Botanik*, II, p. 26, 42. It is certainly suggestive to regard the development of organs from various points of view. I cannot, however, regard the attempt of Wettstein as wholly well-founded. It is quite true that among the liverworts, a thallus may arise at times from a leafy stem. I have shown this for *Pteropsiella* (*Cephalozia*) *frondiformis* Spr. (Goebel, *Rudimentäre Lebermoose*, Flora, 1893, p. 84). But the grounds for regarding this true in general for the thallose liverworts appear to me not to be at hand.

chalazogamy, which elsewhere occurs in forms which may be regarded as degenerate; the facts that only a few of the ovules develop further; that at the time of anthesis they are in many forms not yet present; and finally the dicliny of the flowers. There has been much contention over the question whether the androgynous flowers of these forms are to be admitted to be the original form or not. Let us look at, *e. g.*, the *Cupuliferæ*. Most of the forms have diclinous flowers. In *Castanea vesca*, however, androgynous flowers occur regularly: in the male flowers rudiments of the ovary, while in the female flowers staminodia, are often evident. But we know that for reduced organs all gradations occur from nearly complete development to almost entire disappearance. From the formal standpoint, then, the androgynous flowers may, with at least as much justice, be regarded as primitive as the diclinous ones, which more recently have been thus branded.[1] Just this question is, however, fitted to clear up the difference between pure phylogenetic and causal morphology. The latter says: By the mere comparison of forms morphological questions may not at all be decided. We must first of all become more closely acquainted with the forms to be compared, by seeking to determine the conditions under which, in living plants, the configuration of parts is produced. Concerning the flowers of the *Cupuliferæ* the question then arises: is the occurrence of male and female flowers dependent upon different conditions, and are these other than those under which androgynous flowers arise? As a matter of fact, it may be determined that, *e. g.*, in the oak, the female flowers always occur in those parts of the twig which are stronger, that is, better nourished, than those in which the male flowers occur. This offers us, however, only a point of departure for a more exhaustive research. When we know better the relation between the formation of flowers and the total activity of the plant, when we have the ability at will to cause it to produce male, female, or androgynous flowers, when we further know how it is determined that the oak usually brings to development only one out of six ovules, and why the pollen tube follows a different path than the usual, then may we further discuss the question whether the *Cupuliferæ* are primitive or not—for then shall we have better grounds for phylogenetic conclusions than we have at present, and we shall then recognize with great probability the changes which have taken place in these organs as phenomena resulting from changes in the total organization of these plants.

[1] It was chiefly the fact that among the *Gymnospermæ* the flowers are typically diclinous that led to the view that this condition is the primitive one for the lower *Angiospermæ*. In making such comparisons, however, we should always start from the group in question, and not from some other one. In a very great number of cases dicliny is certainly not primitive in angiospermous flowers, so that it appears entirely probable that also in the remaining cases dicliny is to be derived from monocliny.

So, as the matter now stands, we cannot deceive ourselves on this point, that the constructions of the old morphology, although confined almost entirely to *vestigial* series, nevertheless stood on firmer ground than the modern speculations on the question of primitive forms. Starting with a completely endowed form, we can follow the reduction of form through intergradations, and, by reference to vestigial organs, often with convincing certainty. But by what means shall we judge a rudimentary organ? Is it more than a gratuitous assumption, when, as recently was the case, a certain botanist declares the lodicules of grasses to be not a perigone, but a rudiment of a perigone? [1] Whereby may one recognize a rudiment, *i. e.*, the attempt to form something new, an attempt which, however, has remained nothing more? In what way may we distinguish such a rudiment from a vestigial organ? And, finally, after one has broken faith with the old vestigial series, is it not still more of the stamp of formal morphology if he contents himself in arranging forms in series and then comes to a standstill when he tries to decide at which end stand the primitive and at which end the derived forms? At any rate, such a limitation brings out the better the true condition of our knowledge, for such an arrangement of forms in a series is about the best service that formal morphology can do. This service is, to be sure, no small one, for it enhances broad critical comparison, and is, therefore, the result of hard work. But the desire to give this arrangement in series a genetic bearing has oftentimes led us to untenable propositions and explanations. Just as we have little ground for assigning the *Cupuliferæ* to a primitive position, so have we as little evidence for regarding the *Casuarinæ* also in the same light. The latter have been placed by a recent systematist at the apex of his system, because there has been an inclination to find in them a sort of "missing link" between angiosperms and gymnosperms.[2] I may, perhaps, mention that I had regarded such a view

[1] Engler, *Die systematische Anordnung der monocotyledonen Angiospermen.* (*Abhandl. der K. Preuss. Akad. d. Wissensch. zu Berlin*, p. 22.) The reasons advanced by Engler for the view that the primitive flower of the *Gramineæ* was naked are quite beside the mark, as, *e. g.*, when he expresses the opinion that wind pollination indicates that the types of the *Gramineæ* and *Cyperaceæ* are very old. Is, then, the *Plantago* type very old, or *Thalictrum* "older" than the other *Ranunculeæ?* We know that wind pollination has appeared in widely different groups of plants, evidently in part as a reduction of flowers which were not wind-pollinated. A correlation between the flowers and the glumæ, or paleæ, puts Engler on the defense. We see, however, very plainly in many grasses that leaf-organs which have become superfluous as a result of their position, have become reduced. A similar process may have taken place in the perigonal leaves, and the behavior of *Streptochæta* strongly indicates this. (Cf. on this point Goebel, *Ein Beitrag zur Morphologie der Gräser, Flora,* 81. Bd. *Ergänzungsbd. z. Jahrg.* 1895.) The seed and fruit characters of the grasses also are anything but primitive.

[2] Engler (*Syllabus*, Fourth Edition, 1904) has recently yet again placed the *Casuarinæ* at the point of divergence of the *Dicotyledonæ,* although the contention that in their macrospore before fertilization "a rudimentary prothallium, consisting of twenty or more nuclei, arises" cannot be maintained by the earlier researches of Treub, as I have pointed out (*Organographie*, p. 894). Frye (*The*

as incorrect, even before the evidence was adduced by an American botanist (Frye) that *Casuarina* has evidently nothing which marks it off from other angiosperms. Many of my fellow botanists have been inclined to point out as a further example of the fruitlessness of the search for primitive forms those bryophytes which have been regarded by me as primitive; and I readily admit that here also we cannot point out any conclusive evidence for their primitive position, but only for a greater or less subjective probability. Numerous other examples (as, *e. g.*, the supposed primitive monocotyledons) may be pointed out, which show that the phylogenetic morphology has overrated the prospects of results in search for primitive forms, stimulating as this has been.

This may be seen also if we notice the attitude of phylogenetic morphology to the problem which the old morphology dubbed with the not very fortunately chosen name of metamorphosis, and which historically is that of homologies. Here, also, it may be shown that the problems have remained the same, while only the attempts to reach a solution have changed.

The idealistic morphology believes that all organs of the higher plants may be traced back to caulome, phyllome, and trichome; it conceived this process not as a real one, but was content with a conceptual arrangement of different plant organs in these categories, which were really nothing but abstractions.

That thereby the reproductive organs were left entirely out of consideration — these were referred to modifications of vegetative organs — is explained in part by the fact that they occur in the higher plants less frequently as peculiar parts, and often completely disappear in teratological growths, which are with predilection turned to account in theoretical considerations; and in part because of the view that for morphology the function of an organ is a matter of indifference, and that accordingly in morphological considerations it can have no significance whether an organ has developed as a glandular hair, chaffy scale, or as an archegonium, so long as it has developed out of the outer cell-layer of the plant body! This standpoint, which is an obviously sterile one, needs no further special discussion. Let us, on the other hand, see how phylogenetic morphology has come to terms with the problem of metamorphosis. As an example, I select a passage from a prominent American work, in which Coulter and Chamberlain express themselves concerning the leaf structures of flowers as follows:

"While sepals and petals may be regarded as often leaves more or less modified to serve as floral envelopes, and are not so different

Embryo-sac of Casuarina stricta, Bot. Gaz. XXXVI, p. 104) shows that the embryo-sac of *Casuarina stricta* behaves just as in the other *Dicotyledonæ.* Of this paper, however, Engler has taken no notice. The whole of Engler's presentation shows how far the desire to find primitive forms may lead to untenable views.

from leaves in structure and function as to deserve a separate morphological category, the same claim cannot be made for stamens and carpels. They are very ancient structures of uncertain origin, for it is quite as likely that leaves are transformed sporophylls as that sporophylls are transformed leaves. . . . To call a stamen a modified leaf is no more sound morphology than to call a sporangium derived from a single superficial cell a modified trichome. The cases of 'reversion' cited are easily regarded as cases of replacement. Lateral members frequently replace one another, but this does not mean that one is a transformation of the other."[1]

We see that in this verdict the emphasis is laid on the historical development, but at the same time this is pointed out to be unknown to us. With this latter conclusion I am in complete harmony, but the accentuation of the historical-phylogenetic factor has, on the other hand, led to a conception of the ontogenetic problem, in which I can perceive no advance upon the old morphology; there is rather avoidance of the problem than an attempt to solve it. This, however, is connected with the purely formal conception, as the phylogenetic morphology employs it. Let us examine the matter in question. For a long time we have known that often in the room of the stamens — to confine ourselves to these — flower leaves, or foliage leaves, or occasionally even carpels, arise. The idealistic morphology says that this proves that the stamens are "leaves," for these can be modified the one into the other. Coulter and Chamberlain, however, deny that a stamen fundament may be transformed into a flower leaf; they find only a "replacement" of one "lateral member" by another. It should be remarked that "leaves" exist in nature as little as "lateral members." Both notions are mere mental abstractions, not the expression of the facts of observation. We speak of the replacement of one organ by another if these have nothing more in common than the place of origin. Thus we see that in the foliose liverworts a branch often arises in the position of a leaf-lobe.[2] No one has observed any intermediate form between these; the lateral shoot in reality takes only the position of a leaf-lobe. The relation between the stamens and the organs which "replace" them is, however, quite different. We speak of a transformation of an organ A into an organ B when B not only stands in the position of A, but also corresponds with A in the earlier stages of its development, and later strikes out on its own line of development. If this is the case, we should expect to find between A and B intermediate forms which are different according to the developmental stage at which A is caused to develop further as B. To use an analogy:

[1] Coulter and Chamberlain, *Morphology of the Angiosperms*, p. 22.

[2] Goebel, *Rudimentäre Lebermoose, Flora*, 1893, p. 84. *Ueber die einfachste Form der Moose, ibid.* 76, 1892, p. 92.

Replacement and transformation behave as two fluids which are, and two fluids which are not, miscible; in the first case the inner structure is different, and in the second there is a correspondence. The comparison is a limping one, but still gives us a fair illustration.

As a matter of fact, we do find every intermediate step between stamens and flower leaves, and we cannot doubt that these have come into existence because a stamen, or, in other words, a stamen fundament, has at different stages of its development received a stimulus which has caused it to develop into a flower leaf. We find correspondingly, that the earlier developmental stages of a stamen and a flower leaf are parallel throughout, while in the above-cited example of the branch and a leaf-lobe of a Jungermanniaceous liverwort their developmental histories are throughout different, as is shown by the arrangement of cells. In the case of stamens, therefore, there occurs not a replacement, but a transformation. And, indeed, a limited one. Not any "lateral members" you please may arise instead of stamens, but only and always those which we subsume under the concept leaf, because they evidently have peculiarities in common. Besides, there are also normal flowers which exhibit all intergradations between flower leaves and stamens. The former Coulter and Chamberlain would regard as leaves, the latter not; where, however, is the line of separation between them?

From the limited power of transformation possessed by organs it results that in causal morphology the problem is, then, not a phylogenetic, but an ontogenetic one. Whether sporophylls or foliage leaves are the older phylogenetically may be disregarded. For it appears more important first to determine why the power of transformation is limited, why a shoot-thorn or a shoot-tendril may be transformed only into a shoot, a stamen or a carpel only into a "leaf;" and second, what conditions are determinative thereto.

The first step toward the solution of the problem is that we learn to call out experimentally and at will such transformations as we have heretofore occasionally observed as "abnormalities."

This has been successful in experimental morphology in a great number of cases, and in the future will be still more so. To be sure, we are still unable to induce the transformation of stamens into flower leaves at will, — we only deceive ourselves when we believe that the art of the plant-breeder has succeeded in doing this, for in reality all he has done is to isolate such races which have occurred in nature with more or less doubled flowers, — and in this regard we stand in contrast to the fungi and insects, the activities of which, as Peyritsch and others have shown, often — unconsciously of course — call forth such transformations.[1] Yet it has been possible

[1] The literature is presented in Goebel, *Organographie*, part I, p. 165.

to change scale leaves (cataphylls) and sporophylls into foliage leaves, inflorescences into vegetative shoots, and, *vice versa,* plagiotropous into orthotropous shoots, hypogæous into epigæous, not to mention the interesting results which have been obtained by Klebs [1] in his studies of the lower plants.

Let us take, for example, the just mentioned transformations of scale leaves into foliage leaves and of sporophylls into sterile leaves. Here developmental study and experiment immediately encroach on each other. Development has shown that, *e. g.*, the bud-scales of many trees which in their definitive condition are very different from the foliage leaves, yet parallel them developmentally in an extraordinary degree; and that many bud-scales possess the fundament of a leaf-blade which has failed to develop and has thus become vestigial.[2] Similarly, the fundaments of the foliage leaf and the sporophyll in *Onoclea* [3] are the same up to a quite late stage of development, beyond which each follows its own course. These facts gave occasion to the question whether or not it were possible to influence the development at will, and so to cause a scale leaf or a sporophyll to grow from a fundament which otherwise would develop into a foliage leaf. It has been shown that such transformations may be occasioned in a simple way, and the developmental correspondence makes such a limited transformation without further difficulty capable of being understood. And since seedlings produce, apart from the cotyledons and certain adaptations in hypogæous germination, only foliage leaves, which are arranged for the work of photosynthesis; since further it is seen that all foliage leaves of one and the same plant, different as they appear externally, yet in reality follow one and the same course of development, which, as we have seen, is remarked also in scale leaves and sporophylls, — I accordingly come to the view that other leaf-organs are derived from foliage leaf fundaments through a change in the course of development occurring at an earlier or later period of growth. This conception has found many opponents, some of them for the reason that they have not been able to free themselves from the purely historical conception of the problem.

But the historical question cannot help us over the ontogenetic problem, any more than the solution of the latter alone can answer the historical question. Even if it were proved in all cases that sporophylls, flower leaves, sepals, etc., are transformed foliage leaves, it would remain undecided that these are phylogenetically older

[1] Klebs, *Die Bedingungen der Fortpflanzung bei niederen Algen und Pilzen*, Jena, 1896. Further, *Ueber willkürliche Entwickelungsänderungen bei Pflanzen*, Jena, 1903.

[2] Goebel, *Beiträge zur Morphologie und Physiologie des Blattes. Botan. Zeitung*, 1880.

[3] Goebel, *Ueber künstliche Vergrünung der Sporophylle von Onoclea Struthiopteris, Ber. der Deutschen Botan. Gesellschaft*, v, 1887, p. lxix.

than the former. This phylogenetic problem, however, is with our present means and knowledge not subject to solution with certainty, while the ontogenetic problem, on the contrary, is. Problems, however, which may not be solved appear to me less important than those which may.

To be sure, the solution of the ontogenetic problem is hedged about with great difficulties. For the results which have already accrued, valuable as they may be, take their importance from the fact that they lay the foundation for the future work: what changes take place during transformation, and upon what outer and inner conditions are they dependent? We may not comfort ourselves nowadays as at one time Goethe could with the view that flowers differ from the vegetative shoot in a refinement of the sap; rather would we know what change of the materials, and what other changes, are connected with the order of successive developmental stages of the flower. This, to us as good as unacquired knowledge, should give us a more penetrating glance into the nature of development than we have as yet had. To just this purpose plants are especially well adapted, for experience has shown us that the development of a plant is not produced as is the melody in a music box, in a definite order, so long as the outer source of power is present to start it; for the experiments of the last few years indicate rather "that the form-relations of chlorophyll-bearing plants are not predetermined in the germ cell, but in the course of development." [1] As a result we can not only arrest development at any particular stage, but we can also cause fundaments to unfold which were previously "latent." Historical morphology has contented itself as regards the unfolding of latent fundaments also with an historical explanation of the facts. The observation, *e. g.*, that instead of the seed scale of the *Abietineæ* under certain circumstances an axillary shoot appears, has been used by prominent botanists to support the conclusion that the seed scale has arisen phylogenetically from a shoot. Such an hypothesis would get beyond the rank of pure supposition if a living or fossil form certainly related to the *Abietineæ* could be pointed out, the cones of which bear in the axils of the cover scales shoots possessed of macrosporophylls. As long as such proof is not forthcoming, we stand opposed to a phylogenetic explanation of this observation, "*kühl bis ans Herz hinan.*" We seek rather to establish the conditions under which the fundaments, which otherwise become seed scales, develop into shoots, and hold before us therewith the possibility that the forbears of the *Abietineæ* could have borne their ovules upon an axillary outgrowth of the cover scales, which, indeed, possessed the ability under certain circumstances which disturbed the normal development to form shoots, but which

[1] Goebel, *Flora*, 1895, p. 115.

phylogenetically does not need to have been at any time an axillary shoot.

The question of the significance of metamorphosis leads us into another field of morphology. The above-cited examples show that the transformation of organs always goes on hand in hand with a change of function. This gives us the occasion to take up a further problem of modern morphology: the relation between form and function. The old morphology believed that it should keep away from this question, because it held that the function of an organ had nothing to do with its "morphological meaning." Just recently we have heard that morphology has to do with "members" and not with the "organs" of a plant. The fact that "members" and "organs" mean one and the same thing, and that for the organism their members are organs, or tools, shows that here again is a purely artificial and therefore untenable abstraction. Morphology stiffens to a dead schematism when it does not take the plant for what it really is, — a living body the functions of which are carried on in intimate relation to the outside world. It was the powerful influence of Darwinism that turned more attention again to the function of single plant organs, for, according to one view, which has many adherents, all form-relations arise through adaptation. D. H. Scott has given clear expression to this view in the sentence, "All the characters which the morphologist has to compare are, or have been, adaptive."

This is a widely disseminated conception, but is by no means as widely accepted. Above all, it must be pointed out that it is not the result of observation, but is a theory, which enjoys by no means general acquiescence. True, the conclusion drawn depends upon the meaning given to the word "adaptive." But, take it as you will, in the Lamarckian or in the Darwinian sense, in reviewing the phenomena of adaptation we come face to face with the problem: are the form-characters fixed adaptational characters solely, or have we to distinguish between organization and adaptational characters? There are several grounds which have led to the belief that organization and adaptational characters coincide. Chiefly the brilliant results which investigation concerning the functional significance of structures as well in the flower as in the vegetation organs has had in the last decade. It was evident that structures to which were earlier ascribed no sort of function yet have such. And if none was found, there yet remained the possibility that the structures concerned had earlier been useful as adaptations. It is, however, clear that we are hereby near to the danger of accepting something as proved which needs rather to be proved. In reality, it seems to me that morphological comparison as well as experiment shows that the distinction between organization and adaptational characters is justified, and that the opinion to which Scott has given expression has arisen from the admission that specific characters have arisen through the accumulation of useful fluctuating variations effected by the survival of the fittest. But we see that in many cases specific characters are not adaptive. If we follow out, *e. g.*, the systematic arrangement of the *Liliifloræ*, we see that the particular groups differ from each other as to whether the ovary is inferior or superior, and whether it later becomes a capsule or a berry, and, if it is a capsule, whether it is loculicidal or septicidal. Concerning these characters one may well ask whether one can bring the berry or the capsule into relation with the question of adaptation; whether it can be shown that the berry-bearing *Liliifloræ* occur or have arisen chiefly in those regions where also occur many birds which devour the berries and thus disseminate the seeds. Such a relation cannot at present be shown to exist. And who would regard the question whether a capsule opens septicidally, as in the *Colchicaceæ*, or loculicidally, as in the *Liliaceæ*, as one which stands in relation to adaptation? The method of opening is conditioned by the structure of the fruit in the *Colchicaceæ* and *Liliaceæ*, but for the scattering of the seed it is evidently quite a matter of indifference. Shall we conclude that in the past it was otherwise?

Here again we are shown that we get along the best when we start out with the observation of the plants which surround us, and not with theoretical assumptions and far-reaching phylogenetic hypotheses. The theory of mutations formulated by De Vries with such brilliant results is the result of this kind of patient and step-by-step observation of the now living plant world. The observations of De Vries show us that specific characters arise not through the accumulation of useful variations, but by leaps, and have nothing at all to do with direct adaptation. Such as are disadvantageous in the struggle for existence are weeded out. But selection cannot effect the origin of specific or organization characters as such, and this makes it clear to us why — from the human standpoint — one and the same problem may be solved in such different fashions.

The mutation theory of De Vries limits itself to that alone which the observation of the present moment can come at, to the origin of the so-called "minor species." But how the division of the plant kingdom into the larger groups has come about, how it has happened that the "archetypes" have reached such marked development and others have died out or remained in abeyance, are further problems, the solution of which may not so soon be looked for. For this, however, the more intimate knowledge of the factors which regulate the development of the individual from the egg-cell to the ripening of the fruit forms a fundamental starting-point. For this purpose plants are especially suitable, since, on the one hand, because of the possession of a *punctum vegetationis*, they are in later life also provided with embryonal tissue, and, on the other hand, because in their form they are more exposed to the influence of the outside world than the majority of animals.

An especially important means in order to the causal study of development has the research into those phenomena proved itself, which we designate the regeneration of new formations as the result of wounding. The questions, what really takes place when an embryonic cell becomes a permanent cell; the reciprocal influences of separate plant organs, which we call correlation; further, the problem of polarity, stand out with great clearness in the phenomena of regeneration. I can, however, at this moment only indicate the problems, and cannot point out the steps which have been taken toward their solution. A wide vista spreads out before us. The more must we wonder that of the countless botanical papers which appear each year not more than perhaps a dozen are concerned with the problem of development.

Summing up this brief presentation, it should have been shown that morphology, which originally formed a part of taxonomy, later grew apart from it as an independent discipline. Only when it gives up this separate position will morphology take on new life, for such a position is warranted only historically and not in the facts.

The earlier morphologists would have said that morphology has as little to do with the physiology as with the anatomy of plants, which latter, at the time when systematic botany was in the ascendant, they reckoned also as physiology. For physiology was then everything which was not taxonomy. Nowadays it would be carrying coals to Newcastle to point out the significance of the cell doctrine for morphology. For the understanding of alternation of generations, of inheritance, and other phenomena fundamentally important to morphology, the doctrine of the cell has become of basic significance. The same is true in a higher degree for the relation between morphology and physiology, for all other tasks of the descriptive natural sciences are, after all, only preliminary attempts at orientation, which at length lead to experimental questioning, to physiology. Indeed, one may say that morphology is that which is not yet understood physiologically. The separation of the different tasks of botany is not in the nature of things proper, but is only a preliminary means at first to orientate ourselves with reference to the maze of phenomena. The barriers between these tasks must, then, in the nature of the case, fall with further progress. I do not wish to deny the value of phylogenetic investigation, but the results which it has brought forth often resemble more the product of creative poetic imagination than that of exact study, *i. e.*, study capable of proof. If the knowledge of the historical development of plant forms hovers before us as an ideal, we shall approach it only when we attack the old problems of morphology, not simply with the old method, that of comparison, but experimentally, and when we regard as the basal problem of morphology not phylogenetic development, but the essence of development in a large sense. Even if we had the story of development spread out clearly before us, we could not content ourselves with the simple determination of the same; for then we should be constrained to ask ourselves how it has been brought about. But this question brings us straight back to the present, to the problem of individual development. For there is for natural science hardly a more significant word than this of Goethe's: "Was nicht mehr entsteht, können wir uns als entstehend nicht denken. Das Entstandene begreifen wir nicht." It is, then, the task of modern morphology to learn more exactly the factors upon which at this time the origin of structures depends. To this task, for which there was at that time but little preparatory work, consisting of a few important attempts by the gifted Thomas Knight, Wilhelm Hofmeister, who is known to most of us only as a comparative morphologist, did a too little recognized service. For he pointed out, even before this trend of study became apparent in zoölogy, that the ill-designated *Entwickelungsmechanik* pursues essentially the same goal as the causal morphology of botany.

We may regard as a motto this sentence from Hofmeister's *Allgemeine Morphologie*: "Es ist ein Bedürfnis des menschlichen Geistes, eine Vorstellung sich zu bilden über die Bedingungen der Formgestaltung wachsender Organismen im allgemeinen." This is even now the problem of present-day morphology. Comparative consideration, including, of course, the especially important history of development, offers us valuable preparation for the intellectual grasp of the problem, but, above all, for the pursuit of the experimental method.

That the zoölogists also have felt this necessity to strike out into new ways besides that of comparative morphological observation, shows anew that for all organisms the problems are really the same. Let us, then, take for our watchword development, not only as a problem, but also for the methods with which we seek to bring ourselves nearer its solution.

SHORT PAPER

Doctor J. Arthur Harris, of the Missouri Botanical Garden, St. Louis, Missouri, presented a short paper on the subject of "The importance of Investigation of Seedling Stages," in which the speaker epitomized the recent attempts to solve the problem of the phylogeny of monocotyledons by reference to the anatomy of seedlings.

SECTION C — PLANT PHYSIOLOGY

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(*Hall* 4, *September* 22, 3 *p. m.*)

CHAIRMAN: PROFESSOR CHARLES R. BARNES, University of Chicago.
SPEAKERS: PROFESSOR JULIUS WIESNER, University of Vienna.
PROFESSOR BENJAMIN M. DUGGAR, University of Missouri.
SECRETARY: PROFESSOR F. C. NEWCOMB, University of Michigan.

THE Chairman of the Section of Plant Physiology was Professor Charles R. Barnes, of the University of Chicago, who introduced the speakers as follows:

"It is perhaps somewhat unfortunate that the study of living things must be divided so minutely in these modern times. It is a matter of convenience, in certain respects, to separate plant physiology from other divisions of botany and from the study of animal physiology. It is unfortunate, however, in some respects, for the physiology of plants is fundamentally like the physiology of animals. Indeed, the solution of some of the most important problems of physiology must be sought in a study of the simpler phenomena of plants rather than in the much more obscure, because more complicated, processes in animals. Naturally, therefore, papers on animal physiology are likely to be of great interest to the plant physiologist, and papers on plant physiology should be of equal interest to the animal physiologist. Even were physiologists one, however, they would still have to lament their separation from the chemist, on the one hand, and the physicist on the other, since their study is in reality chiefly applied physics and chemistry. While, therefore, in late years there has been a steady specialization and a tendency to express this specialization by the formation of separate sections and societies, students are coming to realize more than ever before the fundamental unity of scientific study and the close relations that exist between what seem to be quite independent branches.

"The modern history of plant physiology begins shortly after the great impulse given to the study of nature by several contemporary events about the year 1860, the most notable of these being the publication of Darwin's *Origin of Species*. Ever prominent in the renascence of plant physiology will be the name of Julius von Sachs, and high upon the list of those who have advanced the boundaries of knowledge in this field will always be the name of the distinguished investigator who honors us with his presence this day. In 1873 Julius Wiesner founded at the University of Vienna an institute for the study of plant physiology, one of the earliest, as it has been one of the most active, of institutes devoted to this subject."

THE DEVELOPMENT OF PLANT PHYSIOLOGY UNDER THE INFLUENCE OF THE OTHER SCIENCES

BY PROFESSOR JULIUS WIESNER

(*Translated from the German by Professor F. E. Lloyd, Columbia University*)

[**Julius Wiesner**, Regular Professor of Vegetable Physiology, University of Vienna, and Director of the Institute of Vegetable Physiology, since 1873. **b.** Tschechen in Mähren, Austria, January 20, 1838. Studied in Technical High Schools, Brünn and Vienna; University of Vienna, 1856–60; Ph.D. 1860; J.U.D. (*honoris causa*) Glasgow, Scotland, 1898; Privat-docent, University of Vienna, 1861–68. Regular Professor, Technic High School, Vienna, 1868–71; *ibid.* Forest Academy, Vienna, 1871–73; Rector Magnificus, University of Vienna, 1898–99. Member of the Academies of Sciences, Vienna, Berlin, Munich, Rome, and Turin, and numerous other scientific and learned societies. **Author of** *Introduction into Technical Microscopy; The Elementary Structure and Growth of Living Substance; Anatomy and Physiology of Plants; Biology of Plants; The Raw Materials of the Vegetable Kingdom.*]

I HAVE received the honor of an invitation to speak before this great International Congress of Arts and Science on the relation of plant physiology to the other sciences. I gratefully accede to the request. When I accepted the invitation I did so, however, with real pleasure, for, I said to myself, I shall see with my own eyes the great progress which the sciences, especially the natural sciences, have made in America, and I shall have the opportunity to speak on a subject with which I have long been busied, and which has, so to speak, become a part of my life.

It happened that six years ago I spoke in public upon this subject on the occasion of my induction into the office of Rector of the University of Vienna. The content of my address at that time has, I believe, not remained unknown to a wider audience, and I may presume that it has become known to my American colleagues through a translation, with which I was honored, and which was published in the Yearbook of the Smithsonian Institution for 1898. They will then understand that I do not desire merely to repeat myself to-day, and will bear with me, if I give my present address a somewhat different turn and content, without losing sight of the main issue, which is to throw light upon the interaction of the sciences and the complete unification of all human knowledge.

The insufficiency of human understanding compels us to move the lever of research within a small area, and for all time the principle of division of labor will hold good, and, by the same token, the parceling off of the field of labor will advance.

But, necessary as this division of labor is, it has its drawbacks as well as its advantages, for it narrows the horizon of the individual worker, and leads not seldom to a cramped idea of the goal of the sciences. It is often to be blamed for a classification of the sciences in the sense that we imagine that we see an assured advantage in a complete separation of fields of work which we sought to arrive at by means of definition.

But, quite on the contrary, the greatest advances in the sciences are to be made through the union of the results gained by individual research. Not alone through the union of our experiences in special lines, but more especially through the incidence of one science upon the rest, is the richest harvest for all concerned to be gained. This interrelation of the realms of study brings it about that the sciences do not separate from one another, as the classifiers would have it, but, as living streams, change their boundaries, and often unite with each other to form larger units. The final goal, which, to be sure, may never be fully reached, becomes ever clearer: all human knowledge, especially all our knowledge of nature, will become bound together into a great unity. This is the leading thought of my address.

In order to brevity, I will not attempt to trace out the early paths of plant physiology. I take up the thread of its development at that point where its advance appeared assured, that is, at the time of the revival of art and science.

The discovery of the New World, and the almost synchronous announcement of the heliocentric world-system, powerfully stimulated research; and the invention of printing, which had been given to the world a short time before, made possible the spread of knowledge in a theretofore unthought-of way, so that the conditions preparatory to the advance of science were supplied in a manner as never before.

Then the spirit was awakened, and bestirred itself in every branch of science. We can quite understand that, as a result of the wide choice of materials for study, a certain irregularity of development in knowledge should appear. But, in spite of such go-as-you-please methods, there grew up a "spirit of the times," more or less unnoticed, which directed the stream of research into more regular channels than the unconstrained impulses to research might lead one to expect. How the genius of single greatness and how the apparently unsuspected ferments and stimuli of the thought of the times acted upon one another in the struggle up new steeps of knowledge, may not at this time be further discussed.

At the beginning of the period which I have in mind, the physicist was the first to enrich our knowledge of nature. Mechanics — including the mechanics of the system of worlds — formed the point of departure for the studies. Soon followed the discoveries in physics and chemistry, which were not then separated as they became at and after the time of Lavoisier. By the physicists were made the first discoveries in plant physiology, by Mariotte in the seventeenth, and Priestley in the eighteenth century. Priestley, who was from our present point of view a chemist, not only discovered oxygen, but was the first to show that this substance is excreted by plants.

These physicists were the forerunners of Hales and Ingen-Housz, the true founders of plant physiology. Hales, by his studies of sap movement, laid the foundation for physical plant physiology; on the other hand, Ingen-Housz, by his discovery that atmospheric carbon dioxid is dissociated by light in green plants, did the same for the chemical aspect of this study.

Thus it was that the foundations for plant physiology were laid by the physicists. The next advance, the firm establishment of the discovery of Ingen-Housz, came through Th. de Saussure, who was, in the language of his colleagues, as well as in our own, a chemist. At the beginning of the eighteenth century there was no relation between plant physiology and botany. The botanists, who were of the stamp of the Linnæan School, were completely engrossed in description, and were quite indifferent to the knowledge of the life of the plant, already well advanced.

The French were the first to show the relation between plant physiology and botany. The great botanist, Augustine Pyrame de Candolle, came under the influence of his elder colleague and countryman, Th. de Saussure. The great significance of plant physiology, which was at that time too closely identified with physics and chemistry, could not have escaped his far-seeing eye, and he hoped to bring the young science into new life by pressing into service the knowledge of the botanist. In addition to his fundamental studies in systematic botany, he was active as an experimenter in the field of physiology; and by means of his *Physiologie végétale* furthered greatly the knowledge of the life processes in plants by his regard for morphological relations, by the assembling of rich materials for observation, and, in general, by the bringing together of botanical (as then understood) and experimental evidence.

To the French belongs the credit of having preserved intact the continuity of plant physiology, which was effected, in addition to De Candolle, by the important physiological research of his colleague, Dutrochet, and by others, until Boussingault, whose activity extends into the period of the general dissemination of plant physiology.

More slowly was the union of this study with botany accomplished upon German soil. The bridge which led from the one to the other was plant anatomy, which, however, shared the fate of plant physiology, in being regarded as something strange within the bounds of the older botany. This is explained, of course, by the fact that plant anatomy did not originate with the botanist.

Plant anatomy was first made possible by the invention of the microscope; in fact, it was this invention which gave the spur to this study. The earliest anatomical observations of plants were made by

Robert Hooke. This eminent colleague of Newton, as is well known, brought the compound microscope to a considerable degree of perfection. Moreover, to test the performance of his instrument, he studied cork and other plant tissues. These incidental observations led this keen-minded man to the discovery of the plant-cell. Malpighi and Grew, however, went much deeper into the subject than Hooke, and, as Hales and Ingen-Housz are to be regarded as the true founders of plant physiology, so, too, Malpighi and Grew, on account of their studies of the inner structure of plants, stand in the same relation to plant anatomy. None of these four, however, were botanists in the sense of the times in which they lived. Malpighi and Grew were rather physicians, and their endeavors to learn the inner structure of plants and animals led them into the then almost completely unexplored field of plant anatomy. The study of life was of much more meaning to these two anatomists than the business which the botanists set for themselves, and so we see that they associated their morphological studies with the problem of life, and this gave many stimuli in the direction of physiology.

This was the situation at the close of the seventeenth century. What Malpighi and Grew did, went, a hundred years later, to the credit of the growing plant anatomy, while plant physiology got no use from it; we have seen, then, that the founders of plant physiology went to work as physicists and chemists; their aim was a pure physics and chemistry of plants; the anatomical knowledge of Malpighi and Grew had not been made use of.

Much later was the bond between plant physiology and anatomy welded. This was accomplished chiefly by the so-called German plant physiologists in the first third of the previous century. These were plant physiologists, as a matter of fact, only in name. Unpracticed in experiment, they stood aloof from the achievements of their above-mentioned greater forerunners, which were quite foreign and incomprehensible to them. The works which they wrote on plant physiology did not show what had been done in this field decades before. And yet the authors of these works have done a great service, in that they furthered the knowledge of anatomy, and out of this sought, in a one-sided way to be sure, to explain the life of plants.

In two ways, however, the advance of plant physiology was helped. First, in that these men established in Germany the relation to botany of plant physiology, and, in the second place, in that they introduced, besides the chemical and physical point of view already had, a morphological one.

The union of plant physiology to botany by means of anatomy is easy to understand, if we note that the anatomists were first of all concerned with the determination of morphological relations, which were at that time, as they still are, of great significance to the systematist. Thus anatomy gained entrance into botany in the beginning of the previous century, while the botanists of that time yet saw something strange in the physical and chemical conception of plants. Men such as Hedwig, Treviranus, Link, Meyen, and others, who belonged to the ascendant school of botanists, went into plant anatomy. The anatomical point of view must have led them to the question of the functional significance of cells, vessels, and tissues, and thus was developed, from the morphological side, the idea of physiological study of the plant body, just as earlier the physiological and the chemical methods had led to the same goal.

It was the plant anatomist, then, who made physiology at home among the botanists, especially in the German countries. The works on plant anatomy of Treviranus, Meyen, and others, which appeared during thirty years of the last century, give us evidences of the spirit of the teachings of that time on the life of plants. The independent observations and conceptions which are to be found in these works bore a one-sided morphological stamp; and all that dealt with the changes of force and materials in the plant had, on the other hand, the character of compilation, in which the unmatured ideas of agriculturists were accorded a larger place than the researches of the above-mentioned physiologists, who had already departed the field of action.

The whole of the botany of that time, as it was carried on in Germany, had a one-sided morphological character. Under such circumstances, plant physiology could not flourish. This one-sidedness gave to botany, especially in Germany, its specific stamp, and even such men as H. von Mohl could not escape the influence of their time, although his clear intellect made better use of the literary inheritance of plant physiology than did his colleagues. His mind, better adapted for the study of nature, led him to question into the field of experiment, in which he started some fundamental lines of work, as, *e. g.*, the study of twining, and of the tendrils of plants. But his strength always lay in anatomy. In even this, where questioning led straight to experiment, he clung as a rule to morphology. An instructive and pertinent example is his relation to the question of leaf-fall. The history of plant physiology and the influence of other studies upon it are reflected so clearly in this problem that I may be permitted a few moments to follow its development.

The physiologists of the earlier epoch had a purely mechanical conception of this phenomenon. They held that leaves dried up at their death, and that their stiffened forms were broken from the twigs by the autumn winds. It was later held that the buds which developed in the axils of leaves enter between them and the stem like a wedge, and force them off. H. von Mohl showed that this and other such naïve conceptions were untenable, and he tried to point out the true state of things. His discovery of the scission layer was a great advance.

Now, for the first time, it was recognized that the loosening of leaves is brought about by an organic process. But von Mohl conceived the question in a one-sided, almost purely morphological way. Ten years later, when plant physiology started its larger development upon German soil, did they for the first time begin to search experimentally for the causes of leaf-fall, and since that time the question has not been allowed to rest, because we have sought to come at a complete solution by means of combined anatomical, physiological, and biological researches.[1]

How much and how long plant physiology suffered in Germany under the dominion of one-sided anatomical study we are taught by the *Anatomie und Physiologie* of Schacht, which was much valued at this time (1856–59). This work is based almost entirely upon morphology; experimental study was relegated quite to the background; the specifically physiological element is not in evidence.

Yet another remarkable point in the development of German plant physiology demands explanation, because it shows that, as a result of meaningless, one-sided handling, disciplines mutually necessary, instead of helping, have hindered each other. I refer to the conflict of Liebig with the German plant physiologists.

The humus theory, upheld at the end of the eighteenth century by Hassenfratz, was completely overthrown by Ingen-Housz. Yet it was revived again among the German agriculturists and accepted by the German plant physiologists. Their one-sided morphological conception of the life of the plant and their neglect of the study of their great forerunners explains this peculiar fact. As is well known, Liebig laid the new humus theory to rest, as Ingen-Housz had the old. He did it on the basis of the exact methods of chemistry with yet greater certainty than Ingen-Housz, and also with better results. This was the cause which led to a conflict between Liebig and the German plant physiologists, lasting forty years, which was of no use to science, and only showed that Liebig did not understand morphology and that the plant physiologists did not conceive aright the chemistry of the plant. In one thing both parties were wrong. They did not understand how much each was necessary to the other, if they would really further physiology.

The first botanist who studied and mastered equally anatomy and physiology, and attained that balance between them which is neces-

[1] Wiesner, *Untersuchungen über die herbstliche Entlaubung der Holzgewächse, Sitzungsberichte der Wiener Akademie der Wissenschaften*, bd. 64 (1871). *Ueber die neuesten biologischen den Laubfall betreffenden Studien, s. Berichte der Deutschen Botanischen Gesellsch.* 1904. *Ueber den Sommer-Laubfall, Ueber Treiblaubfall.*

sary for the full fruition of plant physiology, was Franz Unger. It was thus that he did his epoch-making work. There came into play, however, a personal factor, also, which leads us to understand his fundamental importance in the development of plant physiology. He was called in 1849 as Ordinary Professor with Endlicher. He made an arrangement with that great systematist to teach anatomy and physiology, and leave taxonomy to his colleague. The compact was never broken. And thus for the first time in history a real professorship of plant physiology became a fact. A new banner was unfurled in a great university. Thousands of students were introduced by Unger to plant physiology. In Vienna, botany, as an object of learning, took on a new character: it was seen that there was something else besides that science of botany which was known to the privileged few, the knowledge of the inner structure and of the life of the plant. What furtherance is experienced by a science, especially in a great university, when a special chair is devoted to it, every subject to which a similar lot has fallen, has, I suppose, undergone.

Through Unger's work, plant physiology, in the best sense of the word, for the first time became so popular in Austria that the establishment of a special ordinary professorship of this study must have appeared to be justified. After Unger's resignation such was provided, and then followed in its train the Institute for plant physiology. When Sachs (1875) urged special chairs and laboratories for plant physiology as an undeniable help to science,[1] they were already in existence in Vienna and Prag, and the Institute for plant physiology founded in Vienna after the establishment of the special professorship of anatomy and physiology of plants was the first workshop of the kind laid out on a grand scale, which furnished the stimulus for the founding of other institutions of the same kind. To-day there exist in Europe and America well-nigh countless such laboratories, and from their origin dates the great advance of plant physiology in the last thirty years.

These arrangements have, however, been fruitful for the development of our science in a way which demands our special attention. Brought into being in great universities, the laboratories for plant physiology were placed in a centre in which they came into intimate touch with other domiciles of research, so that the stimulating influence of the other sciences could hardly have been escaped. Advancement under this permanent contact became ever more marked. This process has gone on before every one of us, and all who understand will admit that the present condition of our science could not have been realized, and the hope for the future could not have been so promising, if, earlier, plant physiology had remained dependent on

[1] Sachs, *Geschichte der Botanik*, München, 1875, p. 572.

itself alone, and had been deprived of that great share which has to-day been afforded it by science and practice.

Science and practice! How often is their advantageous reciprocity misjudged! But it is just in the realm of plant physiology that their reciprocal advancement becomes clear to the unprejudiced, in spite of the errors which have proved a hindrance to their union for so long. Starting from a purely theoretical point of view, Liebig entered the sphere of practical agriculture, and, after an activity full of vicissitudes in the practical and theoretical trends of thought, led by practical ideas, worked especially at his experimental farm at Bechelbronn in Alsace, and Boussingault worked in the field of plant nutrition, advancing, with the most refined means of research, toward the solution of plant physiology. What these two accomplished for agriculture through their researches, especially in regard to the nitrogenous and mineral foodstuffs of crops, must remain as difficult to estimate as the great advance which plant physiology owes to these two men who established the most intimate bond between chemistry and physiology through the founding of agricultural chemistry.

At the end of the sixties the condition of things was thus. Plant physiology had not only come into relation with botany, but had become, indeed, an integral part of it. Further, plant anatomy, physics, chemistry, and practical agricultural chemistry had come to her assistance. Even animal physiology, now and then at least, came into a relation to physiology mutually beneficial to both, since the interrelation of animal and plant life had been clarified by Ingen-Housz and Saussure. I shall take occasion to return to this question later.

In spite of the efforts of Unger and others, who sought to portray plant physiology in comprehensive works, this knowledge, which had been derived from so many sources, was not yet welded into a real unit. There appeared in 1865 the *Experimental Physiologie der Pflanzen* of J. Sachs, in which was drawn up a critical summary of the sum total of the knowledge gained up to this time. This work gave a great impulse to new research. It was a most seasonable undertaking, which, not only by its rich contents, but also by its incomparably clear and illuminating presentation, did not fail to exert a great effect in the further development of plant physiology. Unger's researches and his scholarly activity and Sachs' *Experimental Physiologie* contributed the most to the fruition of plant physiology in Germany in the second half of the last century.

Thus, although Hales laid down the first guiding principles of plant physiology, we have seen that its further development took place in France and Germany. If we except the discovery made first by Priestley, that oxygen is excreted by plants, — a conclusion clarified and strengthened by Ingen-Housz,— England took no further part in the building up of plant physiology as the product of chemical, physical, and anatomical study. Another great impulse, however, emanated from England, the introduction of the principle of development into botany. This, excepting that of a few forerunners, was the work of Robert Brown.

Although this eminent student dealt with development only as a morphological principle and turned it to account especially in taxonomy, yet his method of viewing the vegetable organism from the standpoint of development at once quickened the study of anatomy, which up to this time had taken into consideration only the mature plant, and must be credited, of course, to physiology. Robert Brown taught the doctrine of ontogenetic development. This, however, paved the way for phylogenetic development, which similarly emanated from England, and had its chief champion in Darwin.

The principle of phylogenetic development was of importance first in morphology. By the appropriation of physiological methods and by the application of this principle to purely physiological matters, this historical conception entered with happy results into our sphere. We ask, nowadays, not only how this form, species, genus, etc., has arisen, but we also set before ourselves the question, with reference to the process of differentiation and life processes, how far these are referable to direct influence and how far to peculiarities which have become fixed by inheritance in the course of generations.

Darwin's great influence on the development of our science is not confined to the historical conceptions of physiological phenomena, and in general to that which is connected with the origin and perpetuation of characters beyond the limits of the individual life, with adaptation and inheritance. His conception of organic life has in manifold other ways furthered the development of our science, especially in that he widened our horizon by a unified conception of the whole organic world.

That to-day there may no limit be drawn between plant and animal physiology, and that we may, with advantage to the botanists and zoölogists, and in general to the study of nature, approach a general physiology, is chiefly referable to Darwin's influence, even though in this particular this great student also had his forerunners.

Fechner, with true insight, had already pointed out the irritability of plants. But he preached to deaf ears: the contemporary physiologists were in the bonds of a purely mechanical conception of plant life. A rich harvest came to Darwin through the *Power of Movement in Plants*, in which he showed that plants, without having nerves, yet are able to receive stimuli, to transmit them, and to react in places which are removed from the point of stimulus.

Thus was indicated the way to make use in plant physiology of the experience of animal physiologists. This late intimate contact of so nearly related disciplines, which earlier had been led up to, and again and again failed of, has shown itself in the highest degree fruitful; and the physiology of irritability, which earlier was pushed forward by Sachs, and later by Pfeffer and his school, and is at the present time in the forefront of interest, is referable to the beneficial influence upon plant by animal physiology. I beg to be allowed to emphasize this influence still more, and to indicate the interaction of these two sister sciences.

In spite of Fechner's earlier suggestion on the point, there is nothing to be found in Sachs' *Experimental Physiologie* on the matter of irritability. The most important and most frequently adduced phenomena, as heliotropism and geotropism, were referred to tissue tensions and similar purely mechanical effects. Almost all plant physiologists followed the path which was pointed out by the gifted morphologist, Hofmeister. Only a few of the most striking movements of plant organs, as, *e. g.*, those of the leaves of *Mimosa pudica*, were spoken of by Sachs as "the so-called phenomena of irritability." He stood in this under the influence of the great animal physiologist, Bruecke, who, in order to get a more comprehensive idea of the life of organisms, took up plant physiology and studied closely the sensitiveness of *Mimosa pudica*.

In his *Pflanzenphysiologie*, still following Hofmeister, Sachs explains positive geotropism as a bending under weight, — that the root-tip as a result of its weight when the root is placed in a horizontal position, bends downward in the subapical part, which is composed of soft, plastic, and tender cells. Sachs says expressly that, just as the end of a piece of sealing-wax bends downwards when the part behind is softened by heat, the heavy and stiff end of the root bends out of the inclined, or horizontal, into the vertical position.

In his later writings this account, which was out of all harmony with the facts of anatomy, was not held to, for the conception of the phenomenon of irritability underwent a total change, doubtless under the undoubted influence of animal upon plant physiology. The way we to-day regard irritability in plants is a reflection of the matter from the animal point of view. Pfeffer took this position in the first edition of his celebrated *Plant Physiology*, and yet more clearly and decidedly in the second edition, recently completed. Nowadays the phenomena of heliotropism and geotropism — not to pass beyond the examples cited — are regarded as those of irritability in the sense of the animal physiologists. The causes of stimulation (gravitation, light, etc.) have been determined, the point of reception shown, transmission of stimuli proved, and the whole course determined in detail. The value which accrued to plant physiology through its union with animal physiology forms a debt which the former is trying to pay to the latter, and which in part has been paid. It was the recognition of heliotropic and geotropic phenomena in plants which guided us to discovery of analogous phenomena in animal organisms. And thus we see that the long-separated and independently parallel disciplines have become united into a more symmetrically developing general physiology.

It seemed as if the doctrine of the cell, so important for physiology, would have had a happier fate than all the other branches of natural science. Its founders, Schleiden and Schwann, had worked into each other's hands. Schleiden regarded this as a fortunate circumstance, which, as he expressed it, "protected the doctrine of cell-life entirely from the one-sidedness of a simply botanical or zoölogical point of view."[1] But it has turned out otherwise. The iron law of division of labor holds good here, also, and only after long-drawn-out special researches in both fields has the conviction grown upon us that experience in one field has something to teach us in the other also. About half a century after the founding of the cell theory the large results of animal histology worked a change. The happy discovery of karyokinesis in the animal cell taught the botanists, who saw their enlightenment near at hand in the study of plant cells, in which traces of karyokinesis had been seen, by means of the tried methods of the animal histologist. From day to day the union of plant and animal histology advanced, and our knowledge of the organic elements gradually became more unified, the condition which Schleiden held as an ideal, and, in company with Schwann, had prepared for.

In the field of botany, morphology and physiology sprang up slowly side by side from the several above-mentioned foundations. That we see at this time interrelations between them indicates a far advanced condition. But this significant union is taking place by no means without contention. There yet sticks in the heads of many morphologists that these two parts of botany will thrive the better the more completely they are separated from each other. Advantageous as the division of labor has been, and as much as the study of details has led to this, it must yet be clear to the far-sighted that the solution of the great questions of plant life is possible only by a morphological-physiological treatment. To express it roughly, we may understand a machine when we take note not only of the structure and form of its component parts, but also of their function and work; so may we get an intellectual grasp of the living plant when we study its morphology in relation to its functions. To make use of all demonstrable morphological facts in the explanation of life processes is one of the most obvious phases of modern

[1] Schleiden, *Grundzüge der wiss. Bot.*, Vierte Aufl., Leipzig, 1861. Vorrede, p. xi.

plant physiology, and is to be seen in the development of our science clearly enough. One needs only to compare the older works of Sachs with his last book, *Lectures on Plant Physiology*. In the latter work for the first time morphology comes into living relations with physiology, and this is more clearly evidenced by his presentation of anisotropy, in which he makes the attempt to explain the relation between the formation and the direction of plant organs under the influence of constant outside directive forces. Similar attempts to explain the form-relations of plant organs from analogous points of view were made soon after. Everywhere the most intimate relation between form and structure, and function, was sought after. This research was directed not only at causal but also at teleological explanations, for which experimental evidence was, as far as possible, advanced. Schwendener and his school were active in both directions, furthering the union of morphology and physiology, and thus laying the foundations for a physiological plant anatomy.

The increasing invigoration of physiology by morphology has in more recent times been of the same importance for the further development of our science as the influence of Darwin's basic idea of phylogeny was to numerous problems concerning plant life. The question which now stands to the front is, how have forms arisen, and what functions are bound up with morphological relations, and also how we are to distinguish between ontogenetic and phylogenetic. *E. g.*, Has a particular form or a particular tendency of an organ originated with the individual, or is it referable to inherited peculiarities, or is it the product of ontogenetic and at the same time of phylogenetic development?

The study of ontogeny is the peculiar domain of physiology in the narrower sense — that is, the mechanics, chemistry, and physics of the living organism — so far as the development which takes place before our eyes is approachable by direct observation and experiment. That which may be determined inductively concerning the life, the origin and fate of plants and the plant world may be got at only by following the individual development.

The riddle of ontogeny, and the question of phylogeny (which is well-nigh unanswerable by direct methods) open the door of speculation, and the scope of the problems of the origin and development of the organic kingdom are thus discovered. These have stimulated many students outside of the circle of the observational and experimental sciences to seek help, or at least suggestion, in philosophy.

Indeed, at the present time the philosophical element in natural science has come strongly to the front. The reawakening of research in the theory of descent is indeed the chief cause of this modern phenomenon, which, I believe, commenced in the organic natural sciences, and then passed over into the inorganic.

Whatever we may think on the cause of this phenomenon, philosophy has stepped so far to the foreground within the natural sciences that, in discussing the relations of the sciences to the plant physiology of that time, I cannot avoid examining how far philosophy is in debt to our science.

The question what philosophy is has been very variously answered. If we regard it in the widest sense as the science of all being and happening, and especially of the underlying principles, it is then evident that it, or at least part of it, must form a proper constituent of the natural sciences.

The desire to penetrate the ultimate causes of phenomena is deeply rooted in mankind. This desire, as Whewell at one time so truly remarked, is a curiosity to reach beyond the goal, to step beyond the bounds, which shut in the human spirit. Within these bounds rule the experiences of knowledge. Human knowledge shuns everything which is not made sure by experience. Thus the limit is drawn within which philosophy may and can make itself of service in the natural sciences.

He who follows the development of the natural sciences with a comprehensive view must come to the result that a sound philosophy, based upon experience, has always existed in natural science. The problems which many scientific workers have set themselves are indeed of a simple kind, so that a philosophical penetration into the objects dealt with may not have been sought for by them. But the masters, the leaders, have ever been philosophers, so far as they controlled their observations with logical power, bound together scattered observations with an intellectual insight held in check by criticism, and tested by experience the theories which they formulated. Herein, however, is indicated the limit up to which speculation is permissible in natural science. Hypothesis may be used as a means, but is justified only so long as it stands in harmony with experience.

Such philosophy has obtained since the rejuvenescence of the natural sciences, wherefore this period has properly been called the inductive; such philosophy will and must always obtain, because this kind of philosophy is the living element of natural science.

I do not have in mind that philosophy used by students of the natural sciences, but seldom called so by them, when I speak of the help which they have sought for in philosophy, but rather of that of the specific philosophers, or, as I may say, of the speculative philosophy, or, in brief, of "philosophy."

Highly instructive for the relation of philosophy to the study of natural science is the relation of Newton to the previous philosophers. This has been shown by Brewster.[1] The vortex theory of Descartes

[1] Brewster, *Sir Isaak Newtons Leben*, Deutsche Uebersetzung, Leipzig, 1833, p. 276 ff.

was a real hindrance to the acceptance of Newton's theory of the motions of the heavenly bodies. And concerning the assertion that Newton depended upon Bacon, Brewster has shown conclusively that Newton searched out the truth by observation and by experiment in part worked out by himself and partly borrowed from Copernicus and Galileo.

But, in order to speak of the influences of philosophy on botany, must we not point out Schleiden, who, it may be presumed, placed this science upon a new basis? The methodological basis proposed by him, which may be referred back to Kant, had the value of quite setting aside the harmful academic philosophy of Schelling, which caused not a little confusion among the mediocre botanists of that time, and of adhering to exact observation and to the logical presentation of the facts. But the advance of our science by no means took its origin from his philosophical teachings; this was effected by students such as Hugo von Mohl and others. Schleiden's schematization of the cell was a fruitful idea, and his activity, in the sense of Robert Brown in the field of ontogenetic development, brought a rich return. But all this had nothing to do with the Fries-Appelt philosophy, often cited by him, and with his continual reference to Bacon. His criticism, however, often overshot the mark in matters of plant physiology, and has hindered rather than helped on the development of our science. The greater part of Saussure's experiments he cast aside as "completely useless;" the fact that green plants in an inclosed space can, in spite of gas exchange, keep the surrounding air in a condition in which it remains apparently unchanged qualitatively and quantitatively, was regarded as an impossibility, and in spite of Ingen-Housz and Saussure, it was boldly asserted that Boussingault first proved that green plants absorb carbon dioxid in sunlight. Fechner's views in regard to the irritability of plants, with which all physiologists to-day agree, were not only opposed by Schleiden from the philosophical standpoint, but he even scouted them with derision.

The whole literature shows how little use "philosophy" has been to plant physiology. I will touch upon this with only one example, which, however, will show also that students of science themselves enter into abstract thought so far as it is advantageous to them in the solution of their problems. Schopenhauer, in his work, *Zur Philosophie und Wissenschaft der Natur* (1851), broke a lance for the doctrine of vital force. His arguments against the purely mechanical conception of life are completely justified; but it was these same arguments which were advanced ten years ago by Johannes Müller. So far as Schopenhauer and Müller are in accord with one another on this point, the student of science can follow the philosopher. But when he encroaches on the field of metaphysics, and identifies vital force with the will, he can offer nothing further to the scientist.

As often as philosophy has disturbed natural science, as did the so-called nature philosophy in the period of Schelling, has the sound thought of the scientist always repaired the damage which has been done to our science by the misuse of the human mental power.

The marked philosophical movement of to-day in the natural sciences revolves chiefly about the questions of the origin of life, about the vital force, about the alternative mechanism or vitalism, and about the propriety of a teleological conception of nature.

The further our knowledge of facts extends, the greater becomes the gulf between the lifeless and the dead. Schleiden would have it that the yeasts arise spontaneously from the nutritive fluids; even after the epoch-making researches of Pasteur the attempt was made to show that bacteria arise spontaneously. But this is all past, and there is no fact to support the idea that the living can arise from the non-living. A new support for the correctness of this view is to be found in the conception, supported by an immense amount of evidence, that in the organism, also, the organized or living elements can arise only from the living.[1]

The specific philosophers have offered us nothing on the question of origins. For when Kant, with a far-seeing eye, expressed the view that the living may not arise from the non-living, it was the scientist in him that spoke. When, on the other hand, Naegeli supported the idea of *generatio spontanea*, and, indeed, represented the view that this continues without interruption (while the monists are usually content with the once-for-all origin), this eminent man denied the scientist in him, and descended to doctrinaire speculation. So various is the human disposition that the great philosopher Kant expressed himself on the question of primal origin for a whole century, just as the scientist must at the present moment, while so eminently a modern scientist as Naegeli took the position in this matter not simply of a philosopher of the monist type, but rather of a metaphysician. The arguments of E. von Hartmann that there is now no *generatio aequivoca*, because, in view of the stability of both organic kingdoms, this is no longer necessary, had obviously no effect upon scientists.

But the recent attempts of a prominent scientist to bring back the problem into the field of physics and chemistry by making an analogy between crystal formation in metastabile solutions with spontaneous generation was only an intellectual idea without further consequence in leading to a solution of the question.[2]

[1] Wiesner, *Die Elementarstruktur und das Wachstum der lebenden Substanz*, Wien, 1892, p. 82 ff.

[2] Ostwald, *Vorlesungen über Naturphilosophie*, Leipzig, 1902, p. 345 ff.

Thus to-day we are resigned as regards the question of the origin of life, just as the physicist is as to the origin of matter; and as he pursues his studies on the assumption of the existence of matter, so also we do best when we take for granted the living stuff, and study observationally its nature without speculation upon its first origin.

The kernel of the doctrine of vitalism, which we have recently regarded as dead and buried, was forced again into recognition by the great Johannes Müller, after the attempt to reach a purely mechanical conception of life had been wrecked. Truly, we may no longer hold that in the living individual a force reigns which controls everything within. We really see at work within the organism the chemical and physical forces which are active in the inorganic world. But that which within the organism directs the mechanical forces toward a definite goal and unifies harmoniously all that happens within a living individual and leads to a particular purpose (*Enharmony of the Organism*) [1] cannot be understood from our experience with lifeless nature.

It has often been attempted to refer the whole life of plants and animals to psychological manifestations. This is, however, an extreme view, which fails of profit; while the primitive psychical manifestations in the life of plants, particularly with reference to the consideration of Fechner, may be allowed some consideration.

It will be admitted by every far-sighted observer that the purely mechanical conception of life has been set aside, but that, however, there is no reason to take an extreme vitalistic point of view. In order to accentuate the rejection of extreme mechanism in the control of the organism by means of a certainly unprejudiced judgment, I cite the opinion of an eminent physicist and astronomer, which was published at the time when the mechanical view of nature was in vogue, but which has not been properly appreciated. In August, 1868, Frederick A. B. Barnard, in his address at the opening of the Chicago meeting of the American Association for the Advancement of Science, spoke the following words. "The vital principle differs from every form of force known to us, and from every other known property or quality, in that it confers upon the body which it animates a special character of individuality, and in that it is incapable of being insulated or of being transferred from body to body. We know it only through the peculiar organizing power which belongs to it, and which is manifested not merely in the chemical changes which it determines, but in the external forms which the resulting compounds assume." [2]

The manifestation of mechanical forces in addition to that of

[1] Wiesner, *Biologie*, Zweite Auflage, Wien, 1902.

[2] *Presidential Address*, seventeenth meeting of the American Association for the Advancement of Science. Translated into the German by Klöden, Berlin, Weidemann'sche Buchhandlung, 1869.

a specific "principle" in the life of organisms could not be better expressed; and the reference to "individuality" is a pregnant thought with regard to the enharmony evident in every living form.

It seemed as if the last traces of teleology would have been effaced from biology by Darwin's theory of selection. No one has expressed this more clearly than Schleiden, who, always a tireless opponent of every teleological conception, speaking concerning Darwin's doctrine, cried out in triumph at the close of his activity as a student: "Teleology belongs no more to science, but has its place now only in mere talk."[1] His opposition to teleology started from a one-sided, pedantic philosophy, but his disputatious arguments gained great weight with the majority of the botanists of his time, and his influence in this direction has remained, sporadically to be sure, up till our time. Most of the botanists of his time were so overawed by him that scarcely one of them dared to speak of the purposes of organs or of purposeful arrangements in organisms and so on. And this, as a result, worked a desolation in morphology, and made more difficult its union with physiology.

In this also, however, Schleiden by his hypercriticism overshot the mark. For it was just this great scientific movement, which Darwin set up through the rehabilitation of the doctrine of descent, that of necessity placed teleology in its right place. And this teleology, enriched by an immense number of facts, contributed materially to the advance of the biological sciences. It has also brought it about that eminent and scientifically educated philosophers, such as Wundt, enforced again the recognition of teleology together with causality. In this the reaction of natural science upon philosophy is only slightly indicated. It extended, however, much further, for the rehabilitation of the theory of knowledge is the result of the advancement of natural science; and the coöperation of eminent scientists, such as Boltzmann, Mach, Ostwald, Reinke, and other also scientifically trained philosophers, shows, in the building up of the theory of perception, how science entered this field to its advancement.

That which in the teleological conception concerns transcendentalism we leave to the specialists in the theory of knowledge. We stand on the ground of experience, and permit of metaphysics, as we have said above, only as a source of helpful ideas, which, however, may be permitted only when they do not negate experience, and only so long as they prove themselves useful in opening up to us new directions for inductive research. If through this kind of scientific operation the clear area within which we move appears to be limited within narrow confines, yet our advance within them is the more certain.

[1] Schleiden, *Grundzüge der wissenschaftlichen Botanik*, Vierte Auflage, Leipzig, 1861. Vorrede, p. viii.

The wanderings of the academic philosophers on the extreme limits of human knowledge, and even beyond them, lead only to transitory results, which in turn may be called into question, while science advances steadily in its development. A celebrated physicist and thinker has said that sound human understanding is a lasting product of nature, while philosophy is a meaningless, ephemeral, artificial product.[1]

Only that philosophy will profit us which has arisen from the true spirit of science, even though it advances in the causal and teleological only by way of description. In the spirit of our descriptive methods let us not, when opportunity offers, withhold from speaking of the purposefulness of organization, or of purposes and goals in the realm of life, as in the adequate observation of a machine. In doing so, we renounce the explanation and exposition of final causes of things and events; this lies beyond the limits of the knowledge of nature and beyond the power of man.

From mathematics we have greater hope for the furtherance of our science. Small beginnings are already visible, which at first attain only to a primitive expression in arithmetical representation of quantitative experiments. A further advance is to be noticed in representing mathematically simple physical relations, *e. g.*, to express the entrance and exit of gases into and out of the plant as phenomena of effusion or gas transpiration, or the graphic representation by means of a system of coördinates of the relation of a phenomenon (*e. g.*, heliotropism) to a variable factor (*e. g.*, intensity of light). When a simplification of the conception of a morphological relation (*e. g.*, leaf arrangement) or of a state (*e. g.*, rigidity or elasticity of the plant body or the use of light to plants) is possible, we use mathematical expressions to advantage, and similarly for precise illustration of certain principles (*e. g.*, by means of the biochronic equation of H. de Vries), etc.

Yet these are, as we have said, only small beginnings. Mathematical calculation plays yet a very minor rôle in plant physiology because, in the lack of deeper knowledge of the facts, everything seems as if so hidden in a cloud that the congeries of active factors may not yet be brought to a corresponding mathematical form; that the setting up of a mathematical formula or equation of any kind from which, upon the basis of adequate observations, future conditions may be inferred, appears not yet possible. Animal physiology has already taken the lead, in that in some questions it uses the differential equation, and so it may be expected that mathematical calculation, after the example of physics, will become an important means of advance in our science.

Almost every problem in plant physiology gives us in the pro-

[1] E. Mach, *Die Analyse der Empfindungen*, Dritte Auflage, Jena, 1902, p. 29.

cess of its solution a reflection of the history of our science, ever showing how changeable its limits are and from what various directions, often unexpectedly, its help comes. A pertinent example has been already advanced by me, — that of leaf-fall. Allow me to give as briefly as possible two other examples of great illustrative power.

The problem of leaf position has been till recently purely descriptive, although treated in part with great mathematical and geometrical precision. Later, by Schwendener, it was brought, as a mechanical problem, out of the field of morphology into that of physiology. Quite recently it has been shown that, with reference to illumination, the simplest positions for lateral and for vertical axes, the approximation of leaf positions to the irrational limits of value are the most purposeful. Thus the problem of leaf position was at first morphological, then physiological, and finally biological,[1] or, as we may more precisely say, ecological, whereby it is, however, not said that it cannot be further advanced from the side of morphology and physiology.

In the second place, our great problem of photosynthesis (carbon assimilation). Priestley discovered the excretion of oxygen by the plant, Scheele that of carbon dioxid. But neither was able to say under what conditions these took place. Ingen-Housz first showed that the photosynthesis correlated with oxygen secretion takes place only in the green organs of plants under the influence of light. The explanations of the chemistry involved which obtained from the time of Th. de Saussure to Boussingault are well known. Anatomy now took a hand, and showed us, in the living body of the chlorophyll grain, the place where photosynthesis takes place. The knowledge of the spectrum of chlorophyll, contributed by the physicist, led to the attempt to study the absorption of light by chlorophyll from the physiological point of view. First it was shown how the pigment chlorophyll by light absorption influences the process of transpiration[2] and then the same in regard to photosynthesis.[3] The reference of fermentation to an enzymatic process has raised the question whether photosynthesis may not be a process of this kind. As you know, we are in the midst of a strife of opinions as to whether or not photosynthesis is a matter bound up with the living condition or has to do merely with an enzymatic process. And now the chlorophyll question wanders into the realm of cosmic physics, in that on the one hand the view is set forth that the correlations between photosynthesis and the life of plants and animals presents itself not as a struggle for the elements or for energy, but as a struggle

[1] *Zur Biologie der Blattstellung, Biol. Centralblatt*, 1903, p. 209 ff.

[2] Wiesner, *Untersuchungen über den Einfluss des Lichtes auf die Transpiration. Sitzungsbericht der Wiener. Akad. d. Wissensch.*, 1876.

[3] The well-known works of Engelmann, Reinke, and Timirjazeff.

for entropy,[1] and on the other side, the attempt has been made to show, on the grounds of observation, what proportion of the energy of the sun which is used on the earth by green plants is rendered available for the life of organisms. I here come to the calculation of Pfaundler and to the beautiful and important researches carried on by Brown and Escombe to determine the "economic coefficient," which have shown approximately how much of the sun's energy is fixed by the transpiration of green plants in the light, and by photosynthesis. It was found that in sunlight far more energy is employed for the purpose of transpiration than for that of photosynthesis, and that, in diffuse light, relatively more energy, in comparison with transpiration, is consumed in photosynthesis than in sunlight. Since we in recent times recognize only green plants as autotrophic, the opinion — entirely problematical, to be sure — may well arise that life upon the earth must have begun with green organisms. Now, however, as you know, it has been shown by Hueppe and Winogradski that certain bacteria also fix carbon dioxid, and are in every way to be regarded as autotrophic. Chlorophyll is, then, not absolutely necessary to photosynthesis; but rather has this become to us, according to our present understanding, in the course of the development of the plant world, a wonderful, purposeful means of building up organic substance under the influence of light.

And yet many more details may thus be advanced, to show that even one and the same problem may be brought to its solution by the most different branches of science.

I have, to be sure, only in the most cursory manner tried to show how plant physiology has arisen under the influence of the other branches of natural science, and, finally becoming a part of botany, was advanced by morphology.

How physiology has come into relation with the other branches of science, especially the mental sciences, and has affected practical life, has already been dwelt upon by me.

In order to complete the picture of the interaction of the special sciences, I would, at the close, draw attention to the fact that, young as plant physiology is, it has been of help to pure science far beyond the bounds of botany.

I may mention the advance which plant geography, at first especially a statistical account of the plant world, has made since it was organized upon physiological and ecological bases by Schimper, Warming, and others. It is no paradox when I say that plant physiology has reacted advantageously upon the further development of

[1] Boltzmann, *Der zweite Hauptsatz der mechanischen Wärmetheorie. Vortrag Wiener. Akad. d. Wissensch., Almanach*, 1886, p. 246. See also L. Pfaundler, *Die Weltwirtschaft im Lichte der Physik, Deutsche Revue*, 1902.

chemistry, physics, meteorology, and climatology, and upon other studies far distantly removed, according to earlier conceptions; and that it will do this with still more advantage in the future. Plant physiology is often in need of things, *e. g.*, on the part of physics and meteorology, which these sciences do not have to give her, so that the plant physiologists are compelled to work independently in these apparently strange fields. I may recall Pfeffer's important discoveries in osmosis, which, as is well known, have been of great importance in the theory of osmotic action.

In order to learn the actual, but apparently highly overestimated mechanical effect of rain upon plants, a close student of this question had need of data which were not to be found in the meteorological literature, and himself determined the weight of the heaviest raindrop, its rate of fall, and its kinetic energy.[1] From this study both plant physiology and meteorology profited. The same plant physiologist, incidentally to his studies of the use of light by plants, contributed to the science of climatology by his thorough observations of photochemical climate.[2]

These are random examples merely, but nevertheless indicate that plant physiology is in condition to render service to the so-called exact sciences.

If I should speak a word for the later advantage to physics through plant physiology, this might seem to be an *oratio pro domo*. For this reason I refer to the remarks of a celebrated physicist. Ernst Mach says in one of his best known works, "Not only may physics help and clarify biology (in the widest sense as the doctrine of life), but biology may stand in this relation to physics. . . . Physics will accomplish yet more for biology, after it has grown by means of the latter." [3]

I hasten to a close. I have not intended to present new facts, but rather to use well-known ones in order to support my leading thought to which I gave voice at the outset.

I have tried to present to you a picture in which the development of plant physiology under the influences of the other sciences is portrayed; but in reviewing it I feel that it is very incomplete.

The disproportion between the extent of my duty and the time at my disposal will explain in part the failure to realize my aim. Still more, however, is this due to the difficulty of my subject, for one must master all the sciences which stand in relation to plant physiology in order to give an effective account of its development. On account of the specialization to which we are all committed,

[1] Wiesner, *Beiträge zur Kenntnis des tropischen Regens, Sitzungsber. d. Wiener. Akad. d. Wissensch.*, 1895.

[2] Wiesner, *Beiträge zur Kenntnis des photochemischen Klimas, Denkschriften d. Wiener. Akad. d. Wissenschaften*, 1896 u. 1898.

[3] E. Mach, *Analyse der Empfindungen*, Jena, 1902, p. 74.

hardly any one is properly fitted to carry out this task. I readily admit that there are many others who could have done this better than I. Yet I believe that I have drawn for you some of the more important outlines of the development of our science.

As a chief result of my analysis I have shown the evidence of continual change, of separation and union, of scientific work. Not only are the results gained in divided labor united within small special fields to the advantage of science. Perhaps of still greater advantage is the contact and union of studies which are apparently heterogeneous. Fruitful ideas and methods come often enough not from the narrowly circumscribed field of study, but to a certain extent from outer and apparently foreign realms. And just in the results thus obtained, the facts teach us that all human wisdom, all which to-day furthers the struggle after knowledge, forms only one great unity, which to the individual comes with more reality the deeper he has gone into science.

Yet one thing I would not leave unmentioned at the close. Out of the depths of the past, science has emerged, at first a mixture of truth and fiction, of the results of study which are often intertwined with strange embellishments, inventions, and dark hints. In the older writings, and further on in the literature up till the present time, — in lessening amount, to be sure, — religious conceptions, or wonder at creation, appear side by side with the results of research. But throughout the conviction rings that these reflections, much as they may be in themselves justified and partake of the noblest aspirations of the human mind, must be separated from science, and belong to another sphere.

And yet another form of vague inner impulse still rules, even though it has already been much suppressed, in the realm of science, — the metaphysical element. A trace of the metaphysical, as salt to the bread, will perhaps always remain, because, as already shown, thoughts which help the weakness of the human understanding are as crutches to the lame. We may be allowed to compromise with these small remnants of a once rampant metaphysics, if we entertain such ideas only so long as they do not come into clash with our experience, and really help us in the sure way of observation. There are indeed optimistic theorists who expect that natural science will reach complete fruition only after the last trace of metaphysics has been eradicated.[1]

[1] E. Mach, *loc. cit.*, p. 7.

PLANT PHYSIOLOGY — PRESENT PROBLEMS

BY BENJAMIN MINGE DUGGAR

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To the very year one century has elapsed since Théodore de Saussure published his remarkable investigations relating to the nutrition of plants and to the influences upon plants of certain well-known physical forces. Although preceded by the publications of Duhamel, Hales, Ingen-Housz, and Senebier, as well as by those in a somewhat different line, by Konrad Sprengel and others, we may look upon the work of de Saussure as a wonderful production for his time and as strikingly indicative of the status of plant physiological problems a century ago. His paper may be regarded in a sense as the original charter or constitution of plant physiology. Fortunately, it is assigned to an eminent and experienced botanical historian to recite the amendments which mark the wonderful growth of this historic instrument. There remains, therefore, the task of suggesting some directions of future growth.

No distinction need here be made between those problems which are readily seen to involve the closest work in such other sciences as physics and chemistry and those which do not show a relationship so close. There is certainly much in physiology which must be based upon physics and chemistry, but when dealing with the causes of the activities of living organisms, it is in relatively few cases that explanations may ever be offered in terms of physics and chemistry alone. Nor is it possible to offer such explanations without the assistance of these sciences. The progress of the work in physiology is indissolubly bound up in the development of other sciences. The benefits are, however, mutual, and as physiology acknowledges the fundamental importance of these related sciences, they in turn must acknowledge the important contributions, often of fundamental nature, which have resulted through physiological investigation.

In such a paper it would be impossible to do more than outline briefly some of the relationships of special problems which, for one reason or another, merit emphasis. In general, the problems in plant physiology have been well brought out and systematized through the monumental work recently completed by Professor Pfeffer. To him the science owes a debt of gratitude which may be acknowledged as well by one who attempts to suggest future work as by the historian. Again, due recognition should be made of those who have in recent years based upon this or any similar topic valedictory addresses before various botanical organizations, — notably, those of Professors Vines, Ward, Barnes, Reynolds Green, and others.

The fact that every cell or organ requires its food materials, or at least its nutrients, in liquid form, readily emphasizes the fundamental importance of those problems suggested by the relation of the plant to solutions. The mechanisms for absorption and the general and special diosmotic properties of the living cell, all of which have been studied with the most consummate skill, have yielded matchless results, yet the rewards for future research show at present no distinct limitations. It has not been possible to determine the nature of the plasmatic membrane which directly or indirectly possesses such marked powers of selection and accumulation. The conditions under which the activities of this membrane may be modified are but poorly understood; and it is, perhaps, quite beyond the present possibilities to determine the mechanism of this modification, for in that must be involved one of the most important vital activities of protoplasm. Perhaps when many more data have been accumulated by a study of plants of diverse habitat, the conditions of this modification may be more clearly distinguished. It is known that continued endosmosis of a particular solute depends largely upon the use or transformation of this solute within, yet it is not always possible to demonstrate any change in the substance absorbed. In any event, it is necessary to ask further light upon the exosmotic resistance of the plasmatic membrane to the accumulation of turgor-producing substances, or, in other words, to a further explanation of what may be termed one-way penetration. To these phenomena the processes of excretion and secretion are closely allied, whether they are ultimately, periodically, or continuously the function of certain protoplasts.

Further chemical knowledge is needed dealing with the meaning of high pressures and of the accommodation of very high pressures in the fungi. As a rule, those protoplasts seem to be resistant to such high pressures which are also resistant to cold, desiccation, and other stimulation. Mayerburg, working under the instruction of Professor Pfeffer, has recently applied himself to a study of the method by means of which the organism may regulate its turgor. It is evident that one of two propositions must be assumed, and that increased turgor may be produced either (1) by the penetration of substances from without, or (2) by substances of strong osmotic action produced within the cell through the stimulative action of external agents. It was determined in this case that in general no absorption of the substances bathing the plant occurs; therefore, osmotic substances are produced within the cell and largely by increased concentration of the normal organic cell products. The extent and method of this capability for turgor regulation are highly important, as is also the general question of the relation of turgor to growth. In recent times some of the important problems in this connection have been well suggested by the work of Rysselberghe, Puriewitsch, Overton, Copeland, and Livingston.

The absorptive systems of plants seem to be admirably adapted for their needs from a diosmotic point of view. Diffusion may, therefore, be sufficiently rapid to supply all demands of the absorbing cells or organs. Nevertheless, the assumption that ordinarily diffusion through the cell and plasmatic membrane is sufficiently rapid properly to provide for the translocation of metabolic products from cell to cell is certainly open to further inquiry. Present knowledge of the translocatory processes is insufficient. Plasmatic connections between cells are now known to be of common occurrence, and this fact has given further interest to the above inquiry. Brown and Escombe are of the opinion that the plasmatic connections are eminently adapted for all of those phenomena which they have found to belong as subsequently mentioned, to multiperforate septa. They claim, further, that with slight differences of osmotic pressure the necessary concentration of gradient for increased translocation would be very simply effected.

Thus far it has been difficult to throw any light upon cell-absorption and selection in many complex natural relationships by calling in the assistance of the dissociation theory and the ionic relationships of the salts in the soil. The external relationships of nutrient salts, or the relative abundance of these in substrata supporting vegetation, constitutes a problem with which the physiologist must be concerned. It is only necessary to glance at the results of work done by various experiment stations in this country to be convinced of the great physiological importance which may be attached to such studies.

Recent results tend to emphasize the importance of considering to a greater degree the physical conditions of the soil. Some have even gone so far as to claim that practically all soils contain a sufficient quantity of plant food, and that the all-important question is the regulation of the water-supply in accordance with the quality of the particular soil. This latter, however, is an error into which few physiologists have fallen. Nevertheless, precise studies upon the relation of plants to the physical characters of soils afford problems which should receive the best attention. Many of the problems are not new, and in a qualitative way, at least, the problem of the relationship of the conservation of moisture and the tilth of the soil to productiveness has been duly appreciated by the best agronomists. We must notice with regret, therefore, that botanists have not always appreciated the importance of such work. Either directly or indirectly the water factor is a chief one in regulating the activities of the living plant and must be considered from every possible point of view.

It may, perhaps, be less a problem than a routine matter to determine the relation of the rate of absorption of salts in the soil solutions to water under the varying conditions of growth and transpiration. Nevertheless, information of this nature is important.

In spite of all the recent work, the physical explanation of the ascent of water in trees is a problem which must be mentioned. The renewed investigations which have been made along this line from an objective point of view will undoubtedly contribute to its eventual solution.

It is a matter of interest that in their studies of the physics of transpiration, Brown and Escombe have found evidence to regard this process also as a matter of diffusion through multiperforate septa, rather than a matter of mass action. It is calculated that by diffusion water may pass out of the stomates to an extent as much as six times the actual amount of transpiration which has been observed in special cases.

The great number of cytological investigations which have been completed within the past ten years indicate notable advancements in a most important field; and this is particularly true with relation to the study of nuclear phenomena. Through this work light has been thrown upon many problems of cell physiology and of development: and as a result of the latter new theories of heredity have been advanced. Nevertheless, the field for investigation has been constantly broadened and many new lines of research made possible. In spite of the excellent results accomplished, there is yet great uncertainty as to the interpretations which have frequently been made. In no field of work, perhaps, is it possible for the personal factor to enter into the results more largely than in this. Again, it is unfortunately true that fixed material has been studied almost to the exclusion of all other and that even general observations relating to the conditions of growth have been omitted in many instances. Much attention has been bestowed upon the minutest details which seem to be of morphological significance in the nucleus; but often the purely physiological side has been insufficiently emphasized. It is quite possible that in different plants the exact method of chromosome division, or the manner of nucleolar disappearance, may not be similar; and it is certainly well known that external conditions may considerably modify the details of spindle formation, and perhaps other details in nuclear and cell-division. The important point in every case is to determine if the same physiological purpose may be accomplished.

It is extremely important, however, to the subject of physiology that the methods which have made possible these cytological advances shall be extended and utilized in developing a knowledge of all of the various activities of the cell. In this way, a clearer insight may be given of many abstruse metabolic processes; and certainly further light may be thrown upon the matter of protoplasmic decompositions and secretions, the production of enzymes and alkaloids, tannins and other products. Going hand in hand with observations upon fresh material, the limitations of micro-chemistry alone should determine the possibilities in this direction of the work.

In such cytological investigations, Fischer's work on the artificial production of effects resembling those seen in fixed protoplasm should be borne well in mind. This work is timely, and may assist in checking irrational developments by forcing a proper regard for a comparison of the effects observed in fixed tissues with those shown by the living material.

There are, moreover, but few directions in which the study of metabolism and metabolic products may not profit from cytological research. A notable instance of what there is to be done is well indicated by the work of the late Dr. Timberlake on the division of plastids and the development of the starch grain.

Photosynthesis is a topic which has received a full share of physiological investigation throughout the past century; yet the problems demanding attention are too numerous for complete enumeration. The mechanism of gaseous exchange in leaves has repeatedly been experimentally proved to be the function of the stomates. After critical physical experimentation, Brown and Escombe have recently reported that the results of their studies of diffusivity through multiperforate septa are closely applicable to the herbaceous leaf with its stomates and substomatic chambers. Assuming their calculations to be correct, and granting that all of the incoming carbon dioxide is removed, it is estimated that with the stomates open the maximum observed rate of fixation of CO_2 in *Helianthus* (which is .134 c.c. per square centimeter per hour) would be only 5.2 to 6.3 per cent. of the theoretical capacity of the diffusion apparatus of the plant. In other words, with a gradient between the outer and inner air of only 5 to 6.5 per cent. pressure, the maximum observed fixation is well accounted for.

Important problems in the general study of photosynthesis may well begin with that of a better knowledge of the structure of the chloroplasts and the constitution of chlorophyll. Neither of these, however, is absolutely essential to further physiological observations of a fruitful kind. One of the questions long ago raised is still pertinent: what is the connection between chlorophyll and the plastid in which it is imbedded? An answer to this question may perhaps afford in time an answer to the general inquiry as to the location of the true photosynthetic property. If chlorophyll is always the same chemically, it is perhaps probable that the first product of photosynthesis may always be the same, although this is not necessarily true. In any case, the chief problems hinge upon the method of decomposition of carbon dioxide and water and the synthesis of the first organic product. Neither the hypothesis of Bayer, Erlenmeyer, Crato, Bach, Putz, nor any other, has, to any considerable degree, been made capable of experimental proof, although that of Bayer has been most generally accepted. Each of these assumptions offers some suggestions for future work. Perhaps it may as well be said that they, to a certain extent, bias future research. Nevertheless, even when the chemical reactions in this synthesis become known it may yet remain problematical how the energy of sunlight, that is, of those rays most absorbed, with wave lengths of 660 to 680 μ, is made available, or whether it is this energy directly or indirectly which is concerned in the decomposition. It has been well assumed that the light-waves may not be immediately serviceable, but only after the transformation into other forms of energy. Further, it is not known to what extent this energy is operative in subsequent transformations. The conditions under which photosynthesis occurs have been worked out with a fair degree of accuracy, the status of these problems having been well set forth by Ewart and others. It is known that when deleterious agents act at a given concentration merely to inhibit the assimilatory function (the cell not being permanently injured) there is no evident change in the chlorophyll, from which it has been inferred that the assimilatory arrest has its origin in the plasmatic stroma. In all cases photosynthesis cannot long proceed except under conditions of health of the protoplasts. Nevertheless, the effects of deleterious agents have not always been studied by very delicate tests, and further attention might be bestowed upon this matter by the use of the photobacterial method, or other delicate methods, recently suggested, for it is of considerable interest to determine the relation of the photosynthetic activity to such agents as compared with other activities.

Recently the effects of temperature on photosynthesis have been carefully worked out by Miss Matthaei. She states that the curve of synthetic activity rises with the increased temperature, that it is in general convex to the temperature abscissæ and somewhat similar to the curve of relation between temperature and respiration. There is a certain maximum for each temperature. It has also been ascertained that there is a certain economic light intensity beyond which there is no increased photosynthetic activity, and doubtless only injury. This is of special interest in connection with some recent work by Weis. Recognizing the facts that plants are of very different types with relation to their light requirements, he has sought to get an expression of their assimilatory energy. He finds that *Œnothera biennis*, a well-marked sun plant, fixes under favorable conditions of temperature, and in direct sunlight, about three times as much CO_2 as in diffuse light (light of one sixtieth to one ninetieth this intensity). On the other hand, *Polypodium vulgare* assimilates in diffuse light somewhat more energetically than in direct, while *Marchantia polymorpha* occupies a position intermediate. This will be welcomed by physiologists as a field for wholesome ecological study, for an extension of such investigations to an analysis of plant associations with relation to the light factor may yield profitable results.

In 1901, Freidel made the surprising report of success in securing outside of the living plant a gas exchange similar to the photosynthetic action of chlorophyll. He was later unable to confirm his previous conclusions, nor were the subsequent results of Macchiata and Herzog concordant. Recently, Molisch has employed upon this problem the photobacterial method of Beijernick. He finds that the expressed sap of certain plants may for a time maintain photosynthetic activity, but since usually the sap loses this power when filtered through a Chamberlain filter, it is believed to be due to the presence of living plasmatic particles. Nevertheless, it is claimed that an exchange of gases characteristic of photosynthesis may proceed in a solution of the leaves of *Lamium album* dried crisp at 35° C. and then "rubbed up" in water and filtered. The observation demands much further study, for it must be remembered that the test is by means of the liberation of oxygen, and Ewart has shown that some bacterial pigments may have the power, of evolving oxygen. In the last-named case the gas evolved appears to be, as he states, "occluded oxygen absorbed from the air by the pigment substance excreted by the bacteria."

It cannot be stated at the present time, however, as was assumed from Freidel's first work, that there is any enzyme concerned in the photosynthetic activity.

To a large extent the problems involved in a study of the assimilation of nitrogen are limited by the very imperfect chemical knowledge of nitrogenous products, and may not, therefore, be very clearly defined. Practically, the whole question of the formation of amides, proteids, or other nitrogenous compounds in plants remains in obscurity. It is known that these are formed in both non-chlorophyllous and chlorophyllous plants, and that while in the former it may proceed in darkness, in the latter, light is apparently required for the most vigorous synthesis. In the latter case it may seem to suggest that there is need of the active coöperation of the chlorophyll apparatus; but here again the influence may be only indirect, since the roots, as well as the aërial parts of chlorophyll-bearing plants, are said to possess, to a certain extent, this synthetic power. Interesting suggestions have been recently made by Godlewski. The part played in photosynthesis by nucleus and cytoplasm, respectively, is unknown and may be important.

Some careful studies have been made dealing with the sources of organic nitrogen in certain of the molds, but owing to the very great variety of fungous habitats, further studies may indicate unusual specialization, — perhaps even to such extent as is now known to be true with the bacteria.

Saida has confirmed and extended the early work of Puriewitsch and others, clearly demonstrating that under certain conditions some of the fungi are able to utilize to a variable degree the atmospheric nitrogen. It would be interesting in this connection to give further attention to various groups of saprophytic fungi. In a public lecture Moore has recently made known the results of remarkably definite experiments showing that the organism (or organisms) of leguminous tubercles assimilates free nitrogen apart from its hosts, and that, therefore, the symbiotic association gives the parasite no nitrogen-assimilating advantages. Moreover, this nitrogen-assimilating capacity increases under conditions of artificial culture, and this increased power is heritable to a considerable extent at least. This is an important fact and deserves further attention.

Recently Reinke, Benecke, and others have focused our attention upon the nitrogen supply in sea-water. They find that the organisms *Clostridium Pasteurianum* and *Azotobakter chroococcum* are found in the ooze of sea-bottoms; and the suggestion is made that the external but nevertheless close association of these micro-organisms with certain marine algæ may explain the power of these algæ to grow so vigorously in situations in which they are found. The nitrogen supply is probably one of the most important problems relating to the marine algæ. It is to be borne in mind, however, that the question of fundamental interest is always that of how these micro-organisms are able to utilize the nitrogen which is absorbed in gaseous state. No such power is known among phanerogams. It has not yet been demonstrated to be possible with the lower algæ, and certainly none of the interesting results so far obtained indicate that it is a very fundamental character of fungi and bacteria. In this connection, perhaps, it may also be stated that nothing whatever is known concerning the method by which carbon dioxide is chemo-synthetically utilized by the nitrite and nitrate bacteria.

There are many interesting problems afforded by the general phenomena of metabolism, with relation both to those products which may be immediately utilized and to those which may be stored up for future use. It is well known that during active growth special foods may be taken out of circulation and stored up. The stimulus to such storage is not easily determined. In many instances it is apparently the protoplasm which is decomposed in order that these storage products may be formed; therefore, so far as possible a study of all protoplasmic decomposition phenomena is especially necessary. The deposition of the cell-plate and the storage of reserve cellulose are especially interesting. It will be extremely difficult to follow the succession of changes involved, yet some information will undoubtedly be gained.

The migration of compounds, particularly of those containing nitrogen, magnesium, and potash, to growing vegetative parts and to the developing seed is most remarkable. The production, whether regulatory or otherwise, of the numerous by-products in the cell, such as tannin, pigments, organic acids, etc., is also of peculiar interest. The functions of some of these compounds must be most important, and should receive further attention. Tannin, particularly, is doubtless of much economic importance in the regulation of turgor and in augmenting the resistance to injurious external agents. Astruc has recently shown that acids are found in the younger parts of non-succulents and mostly in the region of maximum turgescence; and that there is a progressive decrease of such compounds in the older organs. In succulents, moreover, very slight changes in the external conditions materially affect the acid content.

It cannot be expected that all of the information desirable with relation to the composition and action of hydrolyzing and oxidizing enzymes will be obtainable until more is known of the proteids, to which group the ferments seem to belong, or with which they are at least closely related. Whether these enzymes are concerned with the metamorphoses involved in rendering soluble or transforming pectin, proteids, glucosides, starches, cellulose, fats, or sugars, their physiological activities are in the highest degree remarkable, and worthy of the closest study. The problems which relate to their occurrence, composition, production, and action require, however, the combined attention of physiologists and organic and physical chemists. In recent times, through the work of Brown and Morris, Fischer, Green, Prescott, Vines, Loew, Beijerinck, Newcombe, Woods, and many others, these compounds have received renewed attention. It may be that at present too many obscure phenomena are passed over with the superficial explanation that they are the result of enzyme action, and, therefore, require no further consideration. It is known that the ferments are largely concerned with the regulatory production or modification of numerous metabolic products. The activity of each enzyme is circumscribed, yet the power to do work borders upon the miraculous. It is asserted that invertin may invert 100,000 times its volume of cane-sugar, and pepsin may transform 800,000 times its volume of proteids. The chemist is especially concerned with the composition and occurrence of these, but the physiologist is interested not alone in the occurrence and specific action of the enzymes, but also with the effects upon the general metabolism of the individual plant, with the methods and conditions regulating the secretion of these products, and with their vitalities or limiting external conditions. Ferments may be concerned with external cellular digestion, that is, with the solution and absorption of foodstuffs from without, thus necessitating exosmosis, or with intracellular modifications, preparatory to the direct use of the substances modified in metabolism or in translocation. Again, the ferments may be present only at a certain definite period in the life of a cell, produced, undoubtedly, by special requirements and special stimulation.

When isolated, or at least when outside of the cell, many enzymes are most active at temperatures far above those which may be maintained within the living cell. An explanation of this fact is difficult. Comparative studies of their reactions to light, heat, toxic agents, and other stimuli should be made. In the penetration of parasites, cellulose-dissolving ferments are important, but further information is needed before it can be said that the presence or absence of such enzymes to any great extent affects the resistance of certain varieties and species to fungous attacks. It has been stated that the resistance of plants to fungous attacks is due largely to the presence of certain enzymes or toxalbumens present in the cells of the host; and by others it has been suggested that susceptibility is frequently a special property due to the presence of certain oxidases, which are regulated by external conditions.

It has been shown that the mosaic disease of tobacco and other similar diseases are accompanied by certain oxidase ferments which appear to prevent the digestion of reserve food. The ferment is developed in the growing parts of the plant, it may be transferred from plant to plant, and on the decay of the diseased organism, it is supposed to be set free in the soil. It is believed that it is then capable of diosmosis and infection of the young seedling. While it cannot be shown at present that the enzyme is beyond all question the direct cause of the disease, this field of work is certainly one which might yield most interesting results. In this connection it may be stated that peach "yellows" and several other important contagious diseases are believed to be of somewhat similar nature. It is also claimed that the keeping qualities of fruits may bear a certain relation to the amount of enzymes present at the time of storage; and, therefore, a knowledge of the time and conditions of the production of such enzymes would have great economic value.

In general, Czapek found no enzymes to occur in the excretions from the roots of higher plants, and it is now generally believed that the roots of one plant may develop no excretions injurious to neighboring plants, and, therefore, there may be no biological relation between the roots of non-parasitic plants associated in the given plant society. It must be said, however, that the information at hand may not be taken as final. There are yet some peculiar facts with relation to the rotation of crops which may not be readily explained on the grounds of the exhaustion of plant nutrients or of the physical condition of the soil.

The fermentation of tobacco and tea, or hay and manure, involves enzyme actions which in recent times have received some attention, although the problems which are of most physiological importance require solution. The general belief is that in all cases of enzyme action these compounds do not form a part of the substance upon which their action is exerted, but they act as a key in each particular case, unlocking, or rendering labile, a certain organic compound, which is then subject to rearrangement and transformation. This is all, however, too speculative for profitable consideration, although such speculation may have no evil influence if it is not permitted to encourage the reference of all unusual phenomena to an unusually obscure and difficult process.

The early perfection of water-culture methods permitted a careful study of the mineral nutrient requirements in the higher plants. Pure culture methods have afforded a more accurate means of studying the needs of fungi and certain algæ. As usually installed, water cultures of the higher plants contain bacteria, so that they afford only a practical test of the requirements. The problem demands some confirmatory tests, at least, under pure culture conditions, particularly when organic compounds are employed. It is possible to grow, in a limited way, higher plants under pure culture conditions.

With the fungi, exact studies may be made upon the influence of the different nutrients on the general form and upon the production of conidia, etc. It has been found, for instance, that, in the absence of potassium, *Sterigmatocytis niger* may produce no conidia or very curious modifications of the conidiophores. By far the most interesting problems with relation to the mineral nutrients are those which have to do with the rôles of these elements in metabolism. The effect of the lack of one or another element is made manifest by some general macroscopic change, and sooner or later, by disturbing pathological changes and subsequent death. It is reported, for example, that the absence of iron prevents the development of a healthy green color, and a scarcity of potassium is made evident, especially in reduced photosynthesis.

We are yet merely at the threshold of these problems. A cytological and microchemical study of numerous plants in various conditions of culture is needed. Loew has instituted some good work in this direction. He attempted a careful microscopic study of *Spirogyra* under the conditions indicated. Although well rewarded, he has not followed up the result. The problem is, nevertheless, again under serious investigation, and when much time and thought shall have been devoted to it, with the utilization of the best cytological methods available, important results may be anticipated. The possibilities of the future are particularly dependent upon this, that investigation must be made of all macroscopic changes as well as of all demonstrable microscopic changes.

The interrelations of parasites and hosts, or of symbionts, are of such great physiological interest that some of the most significant problems may not justly be omitted in this connection. It has long been assumed that the conditions of nutrition of a host plant determine to a considerable extent its immunity to parasitic attack. Ward was unable to detect in the bromes any modification of resistance due to either high cultivation or to lack of sufficient mineral nutrients.

The results which have been attained with the Uredinaceæ have established the fact of the existence of "biologic forms." This opened a new problem in the study of the Uredinaceæ and it was later ascertained that similar host-restricted forms are present in other groups of the fungi, especially in the powdery mildew *Erysiphe graminis*. Salmon has found bridging host species by means of which the parasite may pass from one species or host to another; for example, the form of *E. graminis* on *Bromus racemosus* is incapable of affecting *B. commutatus*, but does not fail to affect *B. hordeaceus;* and the spores produced on the latter will then affect the previously immune *B. commutatus*. From infection studies it is further found that there are biologic forms among the grass hosts as well. Salmon reports that this restriction of the parasite to certain hosts may be broken down if the vitality of the leaf has been lowered by traumatic means. In this case penetration would result either in the injured area or certainly within the sphere of the traumatic influence. Spores produced by such infections proved capable of infecting uninjured leaves. The application of these results is certainly far-reaching; yet they must be extended and confirmed before a conservative explanation may be advanced. It is undoubtedly more or less in line with the well-known capacity of such fungi as *Botrytis*, *Nectria*, and certain Basidiomycetes to become parasitic under special conditions. Two leading inquiries may be suggested: (1) What constitutes immunity or resistance in the host? (2) What constitutes virulence or attenuation in the parasite?

As the result of practical experiments in cross-inoculation, on the one hand, and of close morphological study, on the other, some investigators have long claimed that there are racial or specific differences between the organisms producing the tubercles on the roots of certain leguminous plants. From the results obtained by Moore (in the U. S. Department of Agriculture) which have been reported but not yet published, I am permitted to recite a further interesting fact of accommodation. When an organism isolated from one host species is grown for a time artificially, under special conditions of nutrition, its host limitations are in great measure broken down, and it may produce tubercles on a variety of leguminous plants. It is likewise conceivable that in the case of certain yeasts the temperatures at which spores are formed, and the specific fermentative activities, may be changed by special conditions of cultivation.

In view, therefore, of the work already accomplished it is certainly evident that the propriety of basing what are termed species upon certain physiological characters has distinct limitations. I do not intend to bring into this paper a discussion of the inadequacy of the present nomenclature system from a physiological point of view. It may be said, however, that it is scarcely possible for the systematist to consider all physiological characteristics or to appreciate the confused ideals of the physiologist.

Stimulated by the marked advancement which has been made in physical chemistry, especially in the knowledge of electrolytic dissociation, the past few years have added much to our fund of information with relation to the toxic action upon plants of solutions of both acids and salts, as well also as of certain non-electrolytes. The work of Kahlenberg and True, Heald, Krönig and Paul, Clark, and others has contributed enough data for an appreciation of the limitations of toxic action. Nevertheless, no broad generalizations are as yet possible. Indeed, it is not generalizations which are wanted, but further experimental data bearing upon the relation to the toxicity of the ions and molecules and their respective interactions.

Studies may well be made dealing with the relation of nutrition to toxic agents, the effects of temperature and other conditions upon such action, and the accommodation of organisms to increasing strengths of deleterious agents. Naegeli's work on the oligodynamic action of copper is beginning to be appreciated, and in one way or another the results have in recent times been repeatedly confirmed. In most cases, however, no allowance has been made for the action of the nutrient salts which may be present in the culture fluid and which may affect in a very dissimilar way two different electrolytes. In this connection it is only necessary to call attention to the toxic action of certain compounds of mercury, in which increased toxicity, due to the presence of small amounts of some other salt of the same acid as the mercury salt used, is indeed quite remarkable. Within the past few months an unusually interesting paper has appeared in which Kanda reports the action of certain toxic agents upon plants grown in pots as compared with those plants grown in water cultures. His important conclusions are as follows: (1) A strongly dilute copper sulphate solution, even 0.000,000,249 per cent, is injurious to seedlings of the common garden pea in water cultures; and neither a solution ten times nor one a hundred times more dilute produced any stimulative effect. (2) In pot experiments with soil, the same seedlings are uninjured when watered twice a week during a period of from five to eight weeks with a solution of .249 per cent; in other words, even after from five to seven grams of copper sulphate were present in each pot. No explanation is offered of this remarkable diversity of action, but within the past few months another paper has appeared which may throw light upon the results given. True has ascertained that finely divided paraffin, quartz-sand, filter-paper, or other insoluble substances are all found to reduce the toxic action of the deleterious salt. It is explained on the assumption of an absorption of the toxic molecules by the surface of the insoluble particles. Increasing the number of grains of sand, for instance, in any toxic solution produced the same effect as increasing the dilution. From the results of these two papers it would seem, therefore, that we have two entirely different sets of conditions to deal with when any test of such action is made in water cultures, on the one hand, and in soils, on the other. If Kanda's results are confirmed, an extensive series of tests with both fungi and higher plants should be made in order to determine some relation which may give a working basis for further comparisons. In fact, much of the work thus far done will have to be reëxamined in the light of these results, for if any precipitate or other solid particles have been present in the solutions, an error will enter into the calculations. The question will also arise if the surface extent of the vessel used in the culture is of any consequence. The practical bearing of these results in the treatment of soils is a matter which may prove of unusual economic interest.

Loew observed that marked injury results when such a plant as *Spirogyra* is placed in a solution of a magnesium salt, or in a solution in which magnesium is in excess. From all of the results obtained Loew has inferred that there is present in all plants requiring calcium an essential calcium protein compound. When magnesium must, owing to the predominance of this element, be substituted for calcium in this proteid compound, there results a lessening of the capacity for imbibition, attended by unfavorable consequences. It has been further ascertained by the work of May, Kearney and Cameron, Kusano, Aso, and others, that there is for each plant a certain more or less definite relation between calcium and magnesium. Nevertheless, further experimental proof is needed before this brilliant hypothesis may be acceptable in its entirety. It may here be noted that in a paper read by the writer before the Society for Plant Morphology and Physiology it is indicated that magnesium compounds exert upon the marine algæ the least injurious action of all nutrient bases. On the other hand, it has not been demonstrated that the marine algæ require calcium.

The general phenomenon of chemotaxy, or chemotropism, demands searching investigation in view of the recent work of Jennings on flagellates, that of Newcombe on root responses, and other studies on the fungi. There is much to be done in determining the effects of heat and cold upon special processes, in a study of the relations of temperatures to other conditions of the environment, and in showing the limitations of accommodation phenomena. In the latter study, moreover, the effects of accommodation upon the general constitution of the organism should be followed. Stimulation at high or low temperatures merely expresses an intensified or modified irritability. It may be observed in this place that death at the supramaximal or subminimal may be due to changes of a very definite nature; but, as Vines has indicated, this means very little. To say that death at the supramaximal is due to the coagulation of an albuminoid as suggested by Kuehne is insufficient. For the immediate effect upon the protoplasm of this high temperature must also be of consequence. The external conditions of temperature of the effects of a modification of conditions are more or less readily determinable; but it has not been possible to follow the internal changes which result. It may be noted that the freezing-point of a plant is lower than that of the expressed sap; yet of course the freezing-point is not necessarily a valuable indicator of injury. The effects of temperature upon reproduction will be treated of later.

The symbiotic relationship of fungus and root to *Mycorhiza* offers a fine opportunity for careful investigation. The studies which have already been made serve only to put the reader in a state of hopeless confusion.

The universal phenomenon of irritability as manifested by trophic phenomena has been a fruitful field of investigation. The general methods of irritable response have been determined; and the best work of such investigators as Haberlandt, Noll, Czapek, Newcombe, MacDougal, and others has more recently been directed to the deeper problems relating to the internal mechanism of response and to the exact methods of transmission of the stimulus, as well as to the immediate changes in the cells affected.

A word may be said concerning the regeneration phenomena, which are strikingly characteristic of the lower groups of plants, but which in the higher plants do not seem to be well emphasized, and are certainly less understood. The regeneration of the root-tip has been best studied. In none of the higher plants has it been possible from a single isolated active non-sexual cell, or a small group of cells, to regenerate the plant.

Although a study of the physiology of reproduction may be said to have had its origin in the early observations of Camerarius, all early studies represented largely only the ecological aspect of the subject. It is only in very recent years that rapid strides have been made in the general physiology of reproduction. The effect of conditions upon the production of antheridial or archegonial thalli, or of pistillate or staminate flowers among diœcious and polygamous plants, has received very slight attention. During the present year Laurent has published the results of experimentation during a period of seven years with the effects of fertilizers, or plant nutrients, upon spinach, hemp, and *Mercurialias annua*. It will be seen that according to his results an excess of nitrogen or calcium has a tendency to produce staminate flowers in the spinach, while potassium or phosphorus tends to increase the production of pistillate flowers. The seed produced on the pistillate flowers of these plants gave a preponderance of female plants; but from these plants, in turn, the seed yielded a larger number of staminate plants. So far as I have been able to learn, it has never been determined if in a case of diœcious perennial plants it is possible by a change of conditions to induce a temporary or permanent change from pistillate to staminate flowers, or *vice versa*. In the same way, the influence of grafting or budding a scion of one upon the other has not been made out, although it is assumed that the flower will be characteristic of the scion.

It is with reference to the effects of external conditions upon the production of sexual and asexual fruiting organs that unusual progress has been made. In this direction a field of great magnitude has been opened by the work of Klebs, and it is evidently being pursued along all possible lines. As yet this work has been extended only to a few green algæ (as, for example, *Hydrodictyon* and *Vaucheria*); several fungi (*Sporodinia grandis* and *Saprolegnia mixta* especially); certain yeasts and bacteria, and finally, to several species of phanerogams. While with the algæ the light relation is of prevailing importance, with the fungi it is more particularly a matter of nutrition or transpiration. As a rule, with the latter Klebs finds the stimulus to reproduction in the failure of the food-supply in the immediate vicinity of growth. That is, beginning with a well-nourished mycelium, a diminution of food-supply, other conditions being constant, usually compels reproduction. A change in the specific chemical content may be effective, and in other cases there are other concurrent stimuli. In the study of phanerogams it would seem that the problem is one which is, as a rule, far more complex. It has, however, been found possible with a few species to produce at will continuous vegetative growth or continuous flowering, to induce fruiting in a well-nourished vegetative shoot, and to incite vegetative growth in a flowering axis. It is probable that all shades of difference will be found in the capability of plants to have these processes distinguished by releasing stimuli; and it remains for the future to determine to what extent this is possible.

The general law which seems to be warranted is, that conditions most favorable for growth do not favor reproduction. The problem, then, is to determine for every organism what are these conditions under which, on the one side, growth, and on the other, reproduction, may occur. Whether, under any circumstances, the complete cycle of development may be run without any change in conditions apparently awaits proof.

In grafting it would seem that seldom, if ever, do any characters of the stock pass into those of the scion except such characters as may be due to the presence of diffusible metabolic products, or products capable of self-propagation upon requisite stimulation. In this manner it has been shown that albinism may be transmitted from stock to scion. Again, Strasburger has indicated that atropin is accumulated in the potato when on a potato stock there is grafted a scion of *Datura stramonium*. It has been found that hardiness in the stock may affect the scion to a marked degree, but here the real problem is to determine what constitutes hardiness.

Fusion possibilities in vegetative cells are more or less common in all groups of plants. In basidiomycetes parallel filaments fuse under many conditions of development, and a pseudoparenchymatous tissue may result. In grafting, the layers which fuse may represent different species or even different genera. Little is known concerning the factors influencing such fusions. Allusion may also be made to the fact that plasmodia of the same species of myxomycetes (at least, when produced in nearly similar conditions) fuse with one another. It should be accurately determined if this is an inherent property of the same race or species only, and if this fusion tendency may be weakened or dissipated by diversity of conditions under which the plants may be grown. The solution of such problems with simple and rapidly culturable organisms may even throw some light upon the more complex problems of self-sterility and prepotence (in the sense in which these terms are used horticulturally) in higher plants — phenomena which may not be explained with present information. It has been found that tomato and tobacco fruits are sometimes formed without pollination; and the same is true of other plants. In certain cucurbits the act of pollination seems to afford a stimulus for the development of the fruit, even the dead pollen serving to call forth this response. Under such circumstances it may well be that other chemical stimuli may produce the same effect. On the whole, there are no more interesting problems in physiology than those relating to pollination, the penetration of the pollen tube, and conditions of fertilization. Many phases of these problems have thus far been studied by gardeners and horticulturists alone.

In this connection may be mentioned another fusion phenomenon of physiological interest, — that of double fertilization in the angiosperms. This fusion of the second sperm nucleus with the endosperm nucleus (itself a compound of two nuclei of the gametic groups) or with one of the polar nuclei, may have a special significance, or it may be merely the expression of the fusion tendency which has not been lost, although the function of the endosperm nucleus may have undergone specialization. In the case of the pine, it will be remembered that the second sperm nucleus frequently undergoes division in the cytoplasm of the egg. What is meant by the fusion of the gametes? This is always a fundamental problem. It may be strictly a matter of the fusion of characters, or it may further be a stimulus to embryonic growth. It is a remarkable fact, however, that this stimulus to embryonic growth does not merely involve the embryo itself. The limitations of the correlations which seem to exist between the mere process of fertilization and incitation to growth in the extra-carpellary structures are extremely complex. On the other hand, the process of fusion is often immediately followed by the resting period.

It would be extremely well if further attention could be directed to the matter of parthenogenesis in the higher plants. Except in the case of Nathanson's studies upon *Marsilia*, little has been done to indicate the conditions which may induce or which may tend to induce this process. In recent years, artificial fertilization, or stimulus to a certain growth of the egg in the lower animals, has been effected by chemical agents, by changes in the density of the solution, and by other means. This work has demanded world-wide attention from animal physiologists. It has been too much neglected from a botanical point of view, although the difficulties involved in similar studies with plants would be, for the most part, immeasurably greater. Yet it is certainly possible to prosecute such studies along the lines indicated.

Except in the case of *Sporodinia grandis*, and perhaps one or two other species of *Mucoraceæ*, mycologists have experienced great difficulty in securing the zygosporic stage of these fungi. The recent paper by Blakeslee, announcing the conditions governing zygosporic formation in this family, seems to open a field for investigation wholly novel and suggestive. The substance of his results is that this family may be divided into two principal categories, designated, respectively, as homothallic and heterothallic, these terms corresponding to monœcious and diœcious forms among higher plants. *Sporodinia grandis* belongs to the homothallic type, both gametes in every union developing from the same thallus. *Rhizopus nigricans* belongs to the second and larger class, the heterothallic type, in which the two gametes are invariably the product of two mycelia, which mycelia are sometimes of diverse vigor. When, in culture, the two strains, as they are termed, grow together, zygospores are abundantly produced along the lines of contact. These are the striking results of this important paper; but other related physiological facts have been observed, and only further investigation can tell whether this is a special case of gametic union in the fungi, or whether similar phenomena may be found to be characteristic of other groups where there is gametic union.

The discovery of Mendel's hybridization studies and the independent confirmatory evidence furnished by De Vries, Correns, and others, all indicate the necessity of differentiating unit characters and of following separately the inheritance of each unit character. The idea which it involves of the purity of the gametes with respect to unit characters, the segregation of unit characters in the formation of the gametes, is one of fundamental importance. Such work has given a marvelous impetus to studies in inheritance. Numerous investigators have followed up this work, but it will be many years, perhaps, before a test of the Mendelian laws can be carefully made with any great number of plants and animals. The exceptional instances already reported of the appearance of mosaic characters and the dissimilarity in the product of reciprocal crosses themselves indicate further fields for experimental research. Only a word need be said bearing upon the phylogenetic side of physiological work, since phylogeny, as well as pathology or ecology, constitutes a separate section of biological science. The admirable work accomplished by De Vries, serving beyond all question to demonstrate experimentally the origin of species by leaps or mutations, necessitates laying further stress upon discontinuous variation as a factor in the origination of existing species of plants. It is to be doubted, however, that most botanists will at present concur in such an opinion as that the evidence advanced is sufficient to disregard or disparage the part which is played by continuous variation in the origination of species. Continuous variation must be manifest by relatively slight variations; and it would be unfair to expect at this time the experimental proof of its efficiency. It may even be assumed that there is a complete series between continuous variations and discontinuous variations, as well, perhaps, as between the possibilities of inheriting immediately or ultimately such variations. Many of the problems in plant physiology are distinctly practical problems. The task of the physiologist is primarily to study the activities of plants irrespective of practical bearing. To have the greatest possible breadth and force, however, the cultivated plant may not be neglected in any of its artificial environmental conditions. It is unfortunate that as yet physiological botany has not been made fundamental to agronomy, horticulture, forestry, and other sciences, arts, or commercial pursuits. Physiology cannot be limited by any practical problems, nor can any sacrifices be made, but a sympathy with commercial endeavor will invigorate the work, will afford equipment, and will contribute towards the common good.

In conclusion, it may be said that present-day physiology, even more than any other section of biological science, is fundamental. Many phases of pathology, ecology, phylogeny, and experimental morphology, especially, may not be clearly differentiated as sections. Broadly conceived, plant physiology concerns itself:

(1) With the relationships of existing organisms, ontogenetically and phylogenetically. Phylogeny would necessarily claim much of this general field, as would also morphology, ecology, and other subdivisions.

(2) With the functions or activities of organs, tissues, and cells, and the interactions and interrelations of these one with another and with external forces. It is here that morphology touches physiology most closely, and here experimental morphology must have its basis.

(3) With the incorporation and excretion of matter, metabolism, and growth, the sources and uses of energy, irritability, and the minute constitution of living matter. In this last are included many of the most fundamental problems, not necessarily problems involving the question "What is life?" but problems concerned with the resolution of those factors and an intimate knowledge of those materials which make life possible.

SECTION D — PLANT PATHOLOGY

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(*Hall* 7, *September* 23, 10 *a. m.*)

CHAIRMAN: PROFESSOR CHARLES E. BESSEY, University of Nebraska.
SPEAKERS: PROFESSOR JOSEPH C. ARTHUR, Purdue University.
MERTON B. WAITE, U. S. Department of Agriculture.
SECRETARY: DR. C. S. SHEAR, U. S. Department of Agriculture.

THE Chairman of the Section of Plant Pathology was Professor Charles E. Bessey, of the University of Nebraska, who opened the Section with the following remarks:

"It gives me great pleasure to preside over this Section of the Congress of Arts and Science, since I have been interested in watching the development of the subject with which it deals from its beginnings in this country. The subject is still so new in American botany that many of us in this room remember when it had no existence. Some of us remember the efforts, about twenty years ago, of a few botanists who felt that the United States Department of Agriculture should undertake a systematic and scientific study of plant diseases and their causes. We recall the formal and informal letters we wrote, and the protesting articles which we published in scientific journals. We remember our gratification, not unmixed with some bewilderment, when the Commissioner of Agriculture acceded to our urgent suggestion by appointing a specialist in agrostology to the position of plant pathologist. Although scientifically illogical, this proved to be a fortunate appointment, and good work was at once undertaken, and rapid progress made in the study of certain plant diseases, accompanied by experiments in regard to the best methods of eradicating them.

"From this time of small beginnings so much progress has been made that to-day this country stands foremost in this department of botany. In the United States Department of Agriculture the Division of Plant Pathology now commands the services of many trained specialists, and, in addition, more than half of the experiment-station botanists are plant pathologists.

"Gentlemen, I congratulate you upon the fact that, while you represent one of the most recent developments of botanical science, it is one which you have pushed with such vigor that in the short period of a score of years it has grown from nothing to its present proportions, and I congratulate you further in that you are engaged in work which is at once scientific and immediately useful to the community. I trust that your deliberations to-day may result in giving still further encouragement and impetus to this department of pure and applied science."

THE HISTORY AND SCOPE OF PLANT PATHOLOGY

BY JOSEPH CHARLES ARTHUR

[**Joseph Charles Arthur,** Professor of Vegetable Physiology and Pathology, Purdue University. b. Lowville, New York, 1850. B.S. Iowa State College, 1872; M.S. *ibid.*, 1877; D.Sc. Cornell, 1886; Post-graduate, Johns Hopkins, Harvard, 1879, University of Bonn, 1896. Botanist, New York Experiment Station, 1884–87; Professor of Botany, Purdue University, 1887. Member of the Botanical Society of America; American Association for the Advancement of Science; Indiana Academy of Science; Society for the Promotion of Agricultural Science; Association Internationale des Botanistes; Torrey Botanical Club; etc. Author of *Plant Dissection; Living Plants and their Properties,* etc.]

PLANT pathology, in so far as it has become a science, is an eminently practical one, and credit must be given for the initiative of its development largely to the stimulating demands of economic interests. The more intelligent and intensive methods employed in agriculture, horticulture, and floriculture during recent years have emphasized the profitableness of making due provision for maintaining the health of a crop and for evading and combating diseases in their multiform disguises and modes of attack. It is the reciprocal stimulus of the cry from the commercial world to the man of science that has led to the present highly creditable and valuable understanding of the causes of many forms of diseases in plants, and of their therapeutic treatment. Although far from being a well-rounded and clearly established science, yet its high standing in the long roll of departments of classified knowledge is widely recognized, and its rapidly increasing growth is as sure to be maintained as the arts of productive commercialism continue to outstrip and dominate those of war.

Pathology of plants, as an independent subject, having its own lines of growth and its own terminology, is of very recent standing. Essentially all the part that rises much above empiricism and natural deduction from cursory observation has come to light within a quarter of a century. Very little that cannot be quite as properly relegated to mycology, morphology, and physiology antedates 1880.

The beginnings of the science as displayed in the earliest works giving an independent treatment of the subject are but little more than a century old. These writings are interesting in showing how carefully and effectively the paucity of facts was displayed upon a nomenclatural scaffolding built in imitation of the ancient edifice of human medicine and surgery. A glance at them will prove not only entertaining, but indicate the early lines through which our knowledge has been derived and the primitive influences moulding its form. A representative work of the early school of pathologists is by von Zallinger of the Austrian Tyrol, whose treatise *De morbis plantarum* appeared in 1773. It is a scholarly and comprehensive work. Here are some of the topics considered: In what does the life and death of plants consist? Plants have diseases; wherein lies the health of plants? What may be called a disease of plants? Unfavorable appearances are indications of disease; how many general symptoms of diseases may be found? How many groups of diseases are there? If I should continue, it would soon appear that the work culminates in a classification of diseases based upon symptoms. The fundamental idea of the work is that when symptoms are correctly understood, knowledge of the disease follows with certainty, and treatment may be prescribed accordingly. The classification of diseases, as stated by the author, follows that of contemporary medicine, modified by the methods introduced by Tournefort and Linnæus. There are five general classes, divided into nineteen orders and eighty-four genera. Thus the second class is called *Paralyses*, and is divided into four orders: *Anorexiæ*, *Adynamiæ excretionum*, *Anaphrodisiæ*, and *Commata*. The last order, *Commata*, embraces three genera, *Apoplexia*, *Lethargus*, and *Lethargus gemmarum*. It is easy to see from the vantage-ground of present knowledge that this is more a classification of ideas than of facts. In truth, although the author recognizes the value of a knowledge of causes, the work does not touch upon the true etiology of any disease, and furthermore does not suggest a single prophylactic or therapeutic measure of even meager worth.

A similar work to the preceding is the second part of J. J. Plencks' *Physiologia et Pathologia Plantarum*, published at Vienna in 1794. But a more progressive work, in that it exhibits a better acquaintance with conditions in nature, is that of the Freiherr von Werneck, head forester, who lived in the Rhine provinces, and in 1807 published a *Versuch einer Pflanzen-Pathologie und Therapie*. Von Werneck philosophized thus: The simpler composition a body has, the fewer driving-wheels contribute to its action, but also the briefer, more obscure, and more involved is the chain of causes that lie at the basis of the movement. In order to be able to recognize each simple driving-wheel, or, what is the same thing, each simple cause, we must know the full connection of each simple condition and the value of the contribution of each simple ingredient to the whole. But the incompleteness of our knowledge of the plant body makes this determination of simple causes impossible.[1] The author goes on to distinguish

[1] Je einfacher zusammengesetzt ein Kőrper ist, je weniger Triebräder zu seiner Bewegung beitragen, je kürzer aber auch, je dunkler und verwickelter ist die Kette von Ursachen, welche den Grund der Bewegung enthalten. Um jedes einzelne Triebrad, oder — welches einerlei ist — jede einzelne Ursache bestimmen zu können, müssten wir den ganzen Zusammenhang jedes einzelnen Verhältnisses und

between immediate and remote causes, and to write learnedly upon many pertinent topics. But the amount of real knowledge of facts is small and inconsequential. Seven substances are listed as all that the author had found serviceable in the treatment of diseased plants during eighteen years of experience. They are: Lime, acids, alkalies, balsams, honey, corrosive sublimate, and mineral water. From perusal of his account one is forced to conclude that not much good was accomplished by the application of these remedies.

One more work should be brought forward in this connection. In 1795 J. M. Ritter von Ehrenfels, living not far from Vienna, published a work on the diseases of fruit-trees, which he addressed to the horticulturists among the middle classes. It was written with enthusiasm and inspired by patriotism and love of nature. Scholastic terms are largely discarded and a familiar but dignified style adopted. A work on the same lines at the present time would find place in the "Rural Science Series" or the "Nature Library." However, as in the other works mentioned, it is very evident that the science of pathology and therapeutics was in its helpless infancy.

There is no need to pursue the examination of the works of the beginners further. Enough has been displayed to show that, for the most part, in trying to systematize what little was known regarding the subject, they made a brave showing with borrowed finery of words. Nevertheless, an efficient terminology is not only attractive at any stage of a science, but in its later development nearly indispensable, in order to express exactly and concisely what has been definitely established. Its need is much felt even at the present time. At the Madison Botanical Congress in 1893, the matter was discussed in detail, and it was agreed that "it is desirable for vegetable pathologists to unite upon an international and purely scientific classification of plant diseases," which should be provided, for the most part, with a nomenclature based upon Greek and Latin roots, and that the common names, used by people in general, should be codified, and so far as feasible restricted in application to definite phenomena. The remarks of Professor Bessey at that time are still pertinent, and still deserve to be put into action. "We have two problems before us," he said. "One is the scientific classification of diseases or pathological phenomena; the other the determination of what are the corresponding vernacular terms used by the people. The first of these, the scientific classification, should be international; the work of deciding upon the ordinary vernacular terms need not be international." Nothing was done at the Madison meeting but outline the subject, and the committee [1] appointed at the time to continue the

den Werth des Beitrags jedes einzelnen Bestandtheils zum Ganzen kennen. Aber die Unvollkommenheit unserer Kenntnisse vom Pflanzen-Körper macht auch diese Bestimmung der einzelnen Ursachen unmöglich (p. 11).

[1] This "Committee on the Nomenclature of Plant Diseases" was composed of

work has made no subsequent report. In returning to the historical survey, we find that the borrowed nomenclature of the early pathologists rapidly fell into disuse, as the subject developed, because unsuited to its needs. Yet at the present time there is no question but that a vast accumulation of observation and deduction could be made more available by a purification of names, due consideration being shown to philology and to that curious, indefinable force to which we all submit, usage. We need not adopt the scholastic terms, but in some cases they might prove suggestive.

Plant pathology is debtor to many sciences for suggestions and foundation material, but the debt to human and animal medicine and surgery is not large, and consists chiefly in the transfer of names, with superficial reasons underlying the application.

The next influence that swayed pathology came from a wholly different quarter, and proved of more than temporary strength. In the publication of the treatises on plant physiology and structure by A. P. de Candolle in France, Schleiden and Sprengel in Germany, and the translations from German texts into English and other languages, observations upon deviation from the normal in plant life found considerable substantial basis upon which to rest. Back of these were the discoveries and doctrines of Malpighi, DuHamel, Hales, and Knight, of the earlier physiologists, and Treviranus, Moldenhawer, and especially von Mohl, of the later physiologists of this period, to give direction and strength to the course of ideas, although their influence upon pathology was only indirect. I am now speaking especially of the period from about 1800 to 1850.

Another influence upon the development of the subject during this time, destined to become greater than all others, was the growing interest in mycology. The fungi that are largely instrumental in producing diseases are the very small or microscopic forms. In the study of the classification of these during the first half of the nineteenth century, Persoon, Nees von Essenbeck, Link, and Léveillé especially deserve mention, while Sowerby, Corda, and the brothers Tulasne furthermore contributed much by way of splendid folio illustrations of a large number of species. The systematic diagnoses of the species were chiefly the work of De Candolle, Chevallier, and Castagne in France, S. F. Gray and Greville in Great Britain, Sommerfelt and Fries in Scandinavia, Link, Wallroth, and Rabenhorst in Germany, and Schweinitz in America. Of these the greatest influence was exerted upon systematic mycology by De Candolle, Fries, and Link. Treatises on pathology became more

Professor Byron D. Halsted, of Rutgers College New Brunswick, N. J., as chairman, and Messrs. W. F. Swingle, L. R. Jones, Chas. E. Bessey, W. A. Kellerman, Geo. F. Atkinson, and B. F. Galloway. It was to report to the botanical section of the American Association for the Advancement of Science. The time of service was not limited. See the *Proceedings* of the Madison Botanical Congress, 1893.

abundant at the last of this period, but were chiefly by German and Austrian botanists. The best of these were by Unger in 1833, Wiegmann in 1839, Meyen in 1841, and Nees von Essenbeck in 1842. In these and other works an enumeration and consideration of the parasitic fungi occupied half or more of the space. It must not be inferred, however, that any clear notion had yet developed regarding the relation which parasitic fungi hold to the host and to the accompanying disease. Throughout this period it was generally maintained that their existence was conditioned by the host. At first it was thought that parasitic fungi could not be reproduced by their spores, but were generated by the fermenting sap of the plant, or by a transformation of the perverted tissues. When it became clear that the spores did reproduce the fungus, it was still asserted that the fungus was a product of the disease and that its form was dependent upon the kind of host, or upon the state of the host at the time it was attacked by the disease. Endophytic species were frequently called pseudo-organisms, and the opinion was general that they might be transformed from one kind into another, according to the state of the weather, degree of moisture, amount of nutrition supplied by the host, or other uncertain factors.

It is not a part of the speaker's purpose to sketch the history of plant pathology, but in a perspective outline to trace the dominant influences that at successive stages of the science bore strongly upon the course and rapidity of its development. We have seen that prior to the beginning of the nineteenth century the science had so little knowledge at command that it might be said to be in its helpless infancy. During the first half of the nineteenth century it made rapid growth, nourished by the pabulum derived from the studies of plant structure and function, and from the systematic study of fungi, although harboring many erroneous beliefs. This period may be looked upon as a lusty childhood, full of activity and promise, but guided by unstable and imperfect theories. The next period extended from about 1850 to 1880, during which there was accumulated much positive knowledge of the fundamental features of the science that gave substantial basis for coming usefulness. It was a period of youth, to be followed by the period of established maturity.

The greatest single service rendered to pathology during this interim of thirty years was performed by De Bary in establishing the fact that healthy plants may be attacked and penetrated by fungi, which may there flourish and propagate, thus disproving the long-held theory that parasitic fungi were emanations of the higher plants. This did not lead at once to a full understanding of parasitism, but it cleared the way for an intimate study of the endophytic fungi. In this line of research De Bary was unmistakably the leader. In 1853 he published his investigations on the rust fungi and the diseases caused by them, with special reference to the cereals and other useful plants; and in 1865 he gave to the world the first demonstration of heterœcism among the *Uredinales.*

Nothing could better show the unprejudiced attitude and clear judgment, together with facility for turning unintentional suggestions to account, which De Bary displayed in his studies, than this demonstration of heterœcism. For nearly a century English and Dutch farmers had been convinced from observation that the cup-fungus on barberry bushes in some manner promoted, or possibly gave rise to, the very unlike wheat-rust. These two forms of fungi are so dissimilar in appearance and structure that professional botanists would not entertain the notion that they were but two forms of the same species. Nearly at the beginning of the century, and more than fifty years before De Bary began his experiments, Sir Humphry Davy, the greatest chemist of his times, and well versed in the natural sciences, said: "The popular notion among farmers, that a barberry tree in the neighborhood of a field of wheat often produces the mildew [English term for rust], deserves examination. This tree is frequently covered with a fungus, which, if it should be shown to be capable of degenerating into the wheat fungus, would offer an easy explanation of the effect."[1] Others before and after Davy recorded similar opinions. After De Bary had shown by sowing spores of wheat-rust on barberry leaves, and raising the cup-fungus, that the views of the English farmer were well grounded, Continental botanists made many additional studies of heterœcious rusts, and in 1880 Professor Farlow started the work in America. But in Great Britain, where the annual field demonstration was so plain as to attract the attention of the unlettered, De Bary's results were discredited for more than a quarter of a century, and almost the only work in heterœcism so far done, unless we include the recent brilliant work of Marshall Ward and his pupils on the transference of the uredo-stage to allied hosts, was accomplished in the decade following 1883, by Plowright of King's Lynn, a physician quite isolated from direct scholastic influences.

In the study of life-histories of rust-fungi, and in the introduction of a culture method of observation now employed among all classes of plants, as well as in many other ways, De Bary contributed greatly to the advancement of mycology. The economic problem of the cereal rusts, for which De Bary supplied an interpretation of the most fundamental unknown quantity, transcends that of all others in plant pathology, if measured by the annual money loss to the cultivator in America, Australia, and possibly other countries. It is yet an unsolved problem. De Bary's services culminated in his

[1] Davy, *Elements of Agricultural Chemistry,* 2d ed., p. 266, London, 1814.

classical work on the morphology and biology of the fungi, published in 1884 at Leipzig, and three years later issued in the English language.

Beside great progress made in mycology during the thirty-year period now under consideration, another subject was started and well advanced, which was to become one of the most important sciences affecting pathology, whether of plants or animals, and destined to exert the greatest influence, furthermore, upon human well-being. Pasteur had prepared the way by his epoch-making researches on wine and beer, and the diseases of silkworms, for many excursions into the new world of the "infinitely little," the mighty pigmy kingdom of the bacteria, discovered by Leeuwenhock a century before, but almost unrecognized until now. It had been shown that bacteria were plants, although their power of rapid movement kept many students from fully accepting the fact, when, at the beginning of this period, Cohn, the distinguished botanist of Breslau, first systematized the flora of this new realm, and established the infant science of bacteriology. Already Koch, then a young physician practicing in the vicinity of Breslau, had placed the question of the bacterial origin of certain contagious diseases of animals beyond doubt by his studies of anthrax, but it was not until the last of the period that any plant disease was definitely shown to have a similar origin. In 1880 Dr. Burrill, of the University of Illinois, published his studies on pear-blight, which he called the anthrax of trees, demonstrating that it was always accompanied by an enormous production of minute, colorless bacteria, and that the disease could be set up in perfectly healthy trees by inoculating a few of these bacteria into the young shoots. As in the case of every important discovery, it required subsequent studies fully to establish the claims of the discoverer, and to procure popular acceptance of the truth. Even to-day, after the lapse of a quarter of a century, there appears to be a lurking suspicion in the minds of most European botanists that, after all, the bacteria accompanying pear-blight are not, strictly speaking, the cause of this destructive disease of pomaceous trees. This is doubtless in part due to the fact that the disease does not occur in Europe and other countries outside of North America, for which our trans-Atlantic fruit-growers have reason to be profoundly grateful, although probably unaware of their good fortune. If our distinguished botanical visitors from across the waters to this Congress will observe the great injury which the disease has produced this year in American orchards, in many places killing outright a majority of the pear-trees, and doing immense harm to apple- and quince-trees, and will let it be known upon their return that the statements regarding this disease are not boastful tales to be classed as characteristic of this endlessly expansible country, but sober facts, they will do a distinct service, not only to their eminent colleagues, but to the whole science of plant pathology. For when important truths are not accepted by the students of a science, the progress of the science suffers. That this first claimant among contagious diseases of plants is truly of bacterial origin is a statement as worthy of acceptance as that two and two make four, without need of mental reservation.

After this digression let us glance at the general treatises on the subject of pathology which went into the hands of the public during the thirty years preceding 1880, for one of the indications of cumulative activity and interest in scientific matters is the production of handbooks. They serve as maps to show the extent of exploration, the direction of advancement, and especially as a record of accepted knowledge, all in addition to their usefulness as practical reference-books for the cultivator.

It may be stated first that essentially all treatises of this period were by German authors, or reflections from German writings. The one work that exerted the greatest influence was by Kühn of Lower Silesia, afterward at the University of Halle, not only because it gave the latest information regarding parasitic fungi, to which the work was chiefly devoted, but because the author poured a hot fire of criticism into the camp of hero-worshipers, who extolled Schleiden and Schacht, both extensive writers upon physiological and economic botany, and Liebig, the agricultural chemist, and who, in admiration of the great and brilliant service these men rendered to science and to economics, were blind to their errors and to the drag upon progress which these errors imposed. He decried the medieval tendency to lean upon authority, and advocated closer study of natural phenomena. "It is the problem of the times," he says, "it is the problem, especially of the younger husbandmen, to progress energetically, to unite science with practice, and to apply the results of the former to the improvement of the latter, for personal profit as well as for the benefit of our fellow men. But it is not words or phrases that will lead us to this, — results, economically important results, must we be able to show; but in order to do this, we must understand that to examine methodically, see clearly, observe sharply, and interpret correctly the natural laws underlying the association of phenomena, is the true fruit of scientific study." [1] The admonition was timely and effective. The

[1] Es ist die Aufgabe der Zeit, es ist die Aufgabe, insbesondere der jüngeren Landwirthe, rüstig fortzuschreiten, die Wissenschaft mit dem Leben zu verknüpfen und die Ergebnisse der ersteren auszubeuten zur Vervollkommnung des letzteren, zum eigenen Vortheil wie zum Nutzen unserer Mitmenschen. Aber nicht Worte und Phrasen sind es, die uns dazu führen, — Resultate, practisch bedeutsame Resultate, müssen wir aufzeigen können, und um dies zu vermögen, müssen wir einsehen lernen, dass methodisch untersuchen, klar sehen, scharf

German investigator and the German cultivator became the foremost promoters of the science and practice of plant pathology, and maintained the supremacy almost, if not quite, to the present time.

Beside Kühn's admirable work issued in 1858, and also a dozen or so small handbooks showing the popular interest, two especially notable works, covering the whole range of the subject as then understood, appeared during this trental period. They were by Sorauer, director of the experiment station at Proskan in Silesia, issued in 1874 and enlarged and improved in 1886, and by Frank, of the University of Leipzig, issued in 1880, both authors afterward continuing their labors in Berlin. The two works are essentially alike in the division of the topics, except that Frank devotes over a hundred pages to harmful insects, while Sorauer, like most plant pathologists of the present time, leaves the consideration of insects almost wholly to the entomologist. Disregarding the chapter on insects, both authors devote approximately one half of their space to parasitic fungi, one third to external influences, such as unfavorable conditions of soil, moisture, air, and food-supply, and the remaining one sixth to wounds and galls. There is no need to go into detail regarding these works; their essential features have been preserved in all general treatises up to the present time, and are familiar to every one having some acquaintance with the subject.

At the beginning of the ninth decade of the nineteenth century plant pathology was a subject for scholars and for those who wished to know the reason for things, but it had no great economic importance. It taught many useful matters, but only in a small way. The part pertaining to parasitic growths was an adjunct of mycology, that arising from non-parasitic causes was an adjunct of plant physiology, and that having to do with wounds and galls was an adjunct of plant anatomy. But as a unified and independent science it had little standing. To-day shows a great change. There is such a vigorous growth in so many directions that as a science it seems unsettled and ill-balanced, but its merit as an important and vital part of useful knowledge has been recognized. It has become a utilitarian science of vast possibilities. Like the subject of electricity, which not long since was a department of physics of only moderate prominence, it has felt the energizing effect of a demand to help in forwarding the great economic enterprises of the times, which are the foundations of commerce. In the early days plant pathology was developed by botanists who had special love for the subject, working at such odd times as their regular duties permitted. To-day it has its organized and independent workers,

beobachten und den naturgesetzlichen Zusammenhang der Erscheinungen richtig auffassen lernen, die wahre Frucht naturwissenschaftlicher Studien ist. — Kühn, *Die Krankheiten der Kulturgewächse*, Berlin, 1858.

and the results are far more numerous and valuable; just as the mineral output of the world has been vastly increased where large corporations have supplanted the individual miners who worked for personal gain and love of wild life.

To start the science into this augmented development required an unusual combination of circumstances. So long as the farmer was content to lose from ten to fifty per cent of his crop of grain from smut, rust, or other fungous diseases, and ascribe it to the vague and uncontrollable action of the weather or the season, no concentration of effort was made to understand the nature of the disease, as a disease, and to invent methods of eliminating it from the fields. It required an epidemic severe enough to bring discomforts and threaten poverty in order to start an outcry that would be heeded, and divert the forces of science into a new channel. Such an occasion was the epidemic of potato disease of 1844 and 1845 in northern Europe, and notably in Ireland, where a famine resulted. But the region did not possess scientific men prepared to cope with the situation. Another such occasion was the introduction of the grape mildew into the wine districts of France. The downy mildew of the grape, common in America, but never epidemic, was first noticed in southwestern France in 1878. By 1882 it had become so destructive that in many vineyards about Bordeaux, where proximity to the ocean kept the atmosphere moist and favorable to fungal growth, the leaves dropped from the vines and the harvest of fruit was almost worthless. Here was a critical situation, and the man to cope with it was not wanting. That man was M. Millardet, professor in the Academy of Science at Bordeaux. A fortunate observation at this time was put to the test during the season of 1883, and through persistent study and experimentation carried on by Millardet, and by others under his direction, and by still others working independently, the most important fungicide yet known was soon in general use, and a great industry saved to France. The substance employed has been called from the first the Bordeaux Mixture, and consisted of lime and sulphate of copper in solution, which was sprayed upon the foliage.

It was the introduction of spraying in the early eighties that gave new life and new direction to the study of pathology. It also shifted the geographic centre of activity in the study of plant diseases from Silesia, where it had remained from the earliest times, westward into France. Nevertheless France was not destined to hold this advantage long.

In September, 1884, the American Association for the Advancement of Science appointed a committee [1] on the "Encouragement

[1] The members of this committee were J. C. Arthur, C. E. Bessey, W. G. Farlow, T. J. Burrill, J. T. Rothrock, W. J. Beal, and C. H. Peck. The following year the

of Researches on the Health and Diseases of Plants," three of its most active members being now members of this Congress. In April, 1885, the committee addressed a memorial to the United States Commissioner of Agriculture, calling attention to the desirability of instituting investigations into the diseases of plants under government auspices. The communication was well received, as were subsequent ones, and in July, 1885, Professor F. L. Scribner of Girard College, Philadelphia, was appointed to begin the work. The first report by Professor Scribner appeared in the Yearbook of the Department for 1886, and amply justified the wisdom of the movement.

Professor Scribner with wise foresight directed his greatest efforts toward a study of the diseases of the grape, enlisted the interest of many able vineyardists, and became familiar with the great activity then manifested in France. In 1887 the French Government commissioned Professor Viala, of the National School of Agriculture at Montpellier, to visit the United States and make an extended study of grape diseases throughout our territory, and in this enterprise Professor Scribner coöperated, the field work extending from June to December.

Thus it came about that the activity in the practical application of all that science had to offer in preventive, palliative, or curative treatment of the diseases of crops, especially of the grape, an activity that had recently attained notable proportions in France and Italy, was transplanted to America at a favorable moment, when the Government began to recognize the important interests to be subserved by thus protecting and increasing the output of the cultivator. This movement received another great impetus in 1888, when the state experiment stations were established by act of Congress, many of them including a botanist on the staff of investigators, whose principal duty lay in the direction of the study and dissemination of information regarding plant diseases. It was at this time and during the next few years that many American botanists went to the German universities for longer or shorter periods, and brought back enthusiasm for deep, critical study of difficult subjects. Still another factor which seems to the speaker of immense importance in this connection is the education of the cultivator in the recognition of diseases and in the comprehension of their causes and the extent of the losses that accrue. This has been effected by the bulletins and other publications issued by the Government and by the state experiment stations, by the return of graduates from the agricultural colleges into the active management of farms, orchards,

committee was reduced to five members by substituting the name of C. V. Riley for the last three; and at the next meeting, in 1886, the committee was discharged, having accomplished the particular object had in view when appointed.

and gardens, by the teachings of farmers' institutes, horticultural societies, and similar organizations, and to a less degree by other agencies. The result attained in twenty years is marvelous. At first only few cultivators could understand the nature of the efforts made in their behalf, and great indifference was shown toward suggestions for warding off or controlling fungous diseases, even when emphasized by abundance of proof and demonstration. But with increase of knowledge has developed widespread interest. The prophylactic and precautionary suggestions emanating from the laboratories are rapidly incorporated into daily practice. Great as is the increase in personal and national wealth, which this change has wrought, even greater is its importance in the reaction which has been exerted upon the growth of the science. It may be true, as many times asserted of late, that America now leads in the development of plant pathology, both as a science and in its application as a useful art, and if so, this laudable situation has been secured by increasing the opportunities for scholarly research and by the coöperation of an educated constituency.

I have said that the introduction of spraying gave new life and new direction to the study of pathology. So successful have been the results that it has furnished a sufficient reason for the expenditure of large sums of money, in both government and state institutions, for equipment and men to carry on the work. The division of plant pathology in the United States Department of Agriculture, founded by Professor Scribner, developed by Dr. Galloway, and now administered by Dr. Woods, has within twenty years grown to commanding proportions, with many laboratory workers and field observers, using during the present year an appropriation of $130,000, entirely apart from what is expended in other departments of the Bureau of Plant Industry. It is safe to affirm that if it had not been possible to show that the efforts of the pathologists were resulting in the saving of many millions of dollars to the country annually, this material growth could not have been secured, and a large part of the fundamental knowledge developed in connection with the work would not have become available, while the general stimulus emanating from conspicuously successful enterprise must have been wanting.

A few words regarding some salient features in the history of spraying will give more concrete form to these statements. I have said that Bordeaux Mixture was the first efficient prophylactic substance employed. Although it had been known for a hundred years that copper sulphate, the active ingredient of Bordeaux Mixture, could be used to free seed-wheat of the germs of hard smut, yet attempts to employ it in other ways in controlling fungous enemies usually resulted in disaster, until the fortunate addition of lime reduced the danger of injury to foliage, and made it the most important agent known to-day for the direct treatment of plant diseases. Many experiments have been tried with a wide range of substances, but none has been found to supplant it, although other preparations of copper, like the ammoniacal solution, are used for special cases when the staining of the foliage due to Bordeaux Mixture is objectionable. The methods of application have been refined and extended, early replacing the coarse whisk-broom first employed, until now a great variety of machinery is in the market, and choice may be had of many kinds of nozzles, and of knapsack, barrel, or power pumps of varied designs.

The general introduction of spraying was hastened by the advent of the Colorado potato beetle, which marched in armies across the country from the western plains to the Atlantic coast in a period of about ten years, leaving the potato-fields a waste of withering stalks. Something had to be done to hold in check these voracious insects, that threatened to do for America what the potato fungus had done for Ireland in 1845. As a result of these strenuous conditions, the arsenite insecticides were brought into use. At first they were applied in powder, but when the Bordeaux Mixture proved serviceable for fungi, it was found that both insecticide and fungicide could often be applied in one operation, and since then the practical work of the entomologist has to a considerable extent run parallel with that of the pathologist.

Success in spraying naturally stimulated inquiry into remedial and protective agents for fungous diseases not amenable to spraying methods. Attention was first directed to a method of protecting wheat, oats, and similar grains from smut, which would be more efficient and less hazardous than the very old one of steeping the seed in a solution of blue stone. In 1887 J. L. Jenson of Denmark brought out a method of applying hot water to the seed, that proved very effective, and was widely adopted. Ten years later H. L. Bolley of North Dakota introduced formalin for the same purpose, which is now extensively employed. It has also been found effective and is easily applied in the prevention of potato-scab, and has recently been used for flax where the presence of a fungus threatened to put an end to the industry.

In this connection a very ingenious method of ascertaining what kinds of fungous spores and how many are attached to the surface of seeds was devised not long ago by Professor Bolley. The seeds to be examined are washed with pure water, which is then revolved at high speed in a centrifuge. The resulting drop of sediment is placed under the microscope, and all the germs, large and small, that were present on the seeds are now clearly visible, providing unmistakable evidence of the fungous parasites infesting the field during the last season, and indicating what should be done to prevent a recurrence of these fungi in the next crop.

But great as has been the service to agriculture and horticulture by this development of spraying and its related operations as well as the reciprocal service to the science itself, yet it is the outgrowth of but one division of the science, and that not necessarily the largest one.

Much work has been done, and still more is contemplated and under way, in the breeding of resistant varieties of various kinds of crops, with the double purpose in view of securing larger products and at the same time evading the destructive attacks of certain fungi, insects, and other small enemies. This work is likely to yield excellent results, especially where parasitic forms show adaptations within narrow limits. It must be borne in mind, however, that our knowledge regarding the range of adaptability of parasites is not large. Even the whole meaning of parasitism is not yet available to guide the plant-breeder. Much progress has recently been made toward a knowledge of parasitic adaptations and variations by the researches of Klebahn, Eriksson, Marshall Ward, and others, on the grain- and grass-rusts. Especially significant in this connection are the results obtained by Ernest S. Salmon at Cambridge University, who found that by mutilating or otherwise partially killing the tissues in the vicinity of the spot on which the spores of the grain mildew, *Erysiphe graminis*, were sown, a "biologic" form of barley mildew could be grown on wheat, which under normal conditions would be entirely immune to it. Moreover, when a form was once established by thus lowering the vitality of an immune host, as we may assume was the main effect of the mutilation, spores from the growth thus produced would infect uninjured individuals. Thus through the presence of a wound a parasitic fungus was enabled to gain a foothold and maintain itself on a crop, wheat in the instance cited, which had before been completely immune to it. This is surely a highly interesting situation. What assurance have we that after years of work in establishing an immune variety of grain or vegetable some mishap, like an untimely frost, a hail-storm, or an army of locusts, may not lower the vitality or cause injuries that will give just the right opportunity for the fungus, which we have taken so much pains to circumvent, to gain a foothold in our supposed immune crop, and profiting by the greater vigor of the new host, become after a short period of adaptation a greater pest than it was to the old varieties. Thus at the end of our effort comes worse disaster than preceded it. The moral of this fable is clear. Pathologists should turn more attention than at present to a study of the conditions underlying parasitism, of the degree of adaptation, and of the range of variation, among fungi which cause the diseases most dreaded among cultivators. There are some abstruse and what to many are theoretical questions which need to receive careful answers in order to supply proper guidance for those working upon avowedly practical problems.

But I am in danger of infringing upon the ground of the speaker who is to follow me. It does not, in fact, come into the province of this discourse to speak of work under way at this time, or to point out the unsolved problems, except to indicate the branches of knowledge whose methods or facts are being turned to account.

I may at this point barely touch upon the aid that cytology is rendering to pathology by the illumination which it brings into the matter of the intricate life-histories of many parasitic fungi. Just at present we are awaiting with much interest the cytological results of investigations into the nuclear history of rust-fungi, in order to determine which sets of spores have merely conidial or vegetative powers, and which have sexual and consequently more intense powers of reproduction. Such knowledge will enable us to direct our attacks upon their activity with greater clearness and accuracy.

Taking a general survey of the field, the advance since 1880 is most largely along the study of parasitic diseases, and especially of the organisms which produce these diseases. It is natural that the life-histories of the fungi should first receive attention, especially the numerous small forms on field crops, and that the work should extend gradually to the large but frequently obscure forms on forest trees, and then to the minute and more obscure micro-organisms, the bacteria, yeasts, and possibly amœboid forms. Up to the present time the energy of investigators has been largely absorbed in studying the inciters of disease; the means by which the assaulting organism overcomes the resistance of the host has received small elucidation, and the nature of the physiological perturbations induced by the parasitic organisms, or by any other cause, is almost an unexplored field.

If I have said little about bacterial diseases, which have been studied with such brilliant success and with such clear and discriminating judgment by Erwin F. Smith of Washington, or of diseases caused by enzymes, to which we were introduced by the researches of Loew, or of the well-marked diseases of unknown origin, such as yellows and rosette of peach-trees, it is that I do not doubt but you will hear them more ably and entertainingly presented by my successor upon the programme. Neither is it desirable that I should discuss the advance likely to be brought about by the new theories and methods in the study of the action of poisons, as these are applied to the explanation of diseases, as well as to the devising of remedies.

In the long list of indebtedness held against plant pathology by various sciences, physiology stands foremost with the largest account, a condition fully recognized as early as the days of A. P. de Candolle, and especially emphasized at the present time. But in close succession follow mycology, anatomy, bacteriology, chemistry, cytology, physics, toxicology, phylogeny, and other subjects in diminishing degree. That the science is largely in an uncrystallized condition, when looked at from our new points of view, is probably the reason why no handbook written from the modern standpoint and covering the whole subject has appeared since 1880, with the exception of the small, introductory, but highly luminous work by Marshall Ward, issued in 1891.

I trust that in this cursory presentation of the history and scope of the science of plant pathology I have made clear some of the lights and shadows that give interest to a subject of great economic and scientific importance.

VEGETABLE PATHOLOGY AN ECONOMIC SCIENCE

BY MERTON BENWAY WAITE

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VEGETABLE pathology is a practical, economic science and is an important aid to horticulture and agriculture. The science of botany began, in its early days, as an economic study of medicinal herbs, but the development of the subject has been mainly along the lines of pure science. There are no higher motives for study than the pure love of knowledge. To discover the laws and facts of plant life, for the satisfaction of knowing, has doubtless been the object of most of the researches of the botanists. Botany is rapidly becoming a practical science, but no one despises more than myself the attitude which assumes that knowledge for its own sake is not worth while attaining. The enthusiasm of the botanist is proverbial. The study was so fascinating that men pursued it for its own sake. In this way the various departments of botanical science have been built up.

Vegetable pathology utilizes all botanical knowledge and turns it to practical account. Doubtless the diseases of plants have been studied to a certain extent as pure science, but the enormous progress of the last twenty years in the study of plant diseases under the support of governments, experiment stations, and other public institutions, has been due to the practical utility of the knowledge obtained. Vegetable pathology calls to its aid all departments of botany as well as entomology, chemistry, physics, geology, and allied natural sciences. How different were the methods of the systematic botanist half a century ago from the investigating pathologist of to-day. The one working in some attic or small room, with his bundles of dried flowers and ferns and his collections in pigeon-holes; the other, with his expensive laboratory facilities, chemical and physical apparatus, greenhouses, gardens, and other equipment. And yet the systematic botanist laid the foundation for pathological work. The early mycologists, even if some of their descriptions were only three lines long, have left us very deeply indebted for the names and classification of the fungi. The working pathologist must know systematic mycology as well as the classification and names of flowering plants. He must be an all-around botanist. A copy of Saccardo's *Sylloge Fungorum* is an essential in every well-equipped pathological laboratory.

Mycology is so intimately connected with vegetable pathology that some have thought the terms synonymous. The parasitic fungus is frequently spoken of as the disease. The fundamental conceptions are distinct, however, even if in practice the work is interwoven. The mycologist studies fungi for themselves; the pathologist for the diseases they produce — in other words, from the standpoint of the host plant. If we acknowledge indebtedness to the early systematic mycologists, what must we say of the life-history of the fungi? To the studies in the biology of the fungi, as worked out by De Bary and his pupils, we trace the direct starting-point of modern investigation work in pathology. By no means are all plant diseases caused by parasitic fungi; yet the fungus diseases are so numerous and important that with their knowledge well under way, we are prepared to understand and distinguish from them the injuries produced by insects and mites, poisons and unfavorable environment, as well as the physiological and other non-parasitic troubles.

Plant physiology is another of the great aids to pathology. Physiology not only enables us to understand the disturbances in growth and nutrition of plants produced by parasitic fungi and other parasites, but it enables us more fully to understand the non-parasitic diseases. Through the researches of Dr. A. F. Woods an entirely new type of physiological disease is known to be produced by the action of enzyms. The study of enzymic diseases is in its infancy, but promises to enable us to unravel some of the most mysterious plant troubles. In this type of disease we have the curious anomaly of non-parasitic diseases which are contagious or at least communicable.

The closely allied subject of anatomical botany is also of great importance to pathologists. Not only is the knowledge of normal plant anatomy necessary in the study of abnormal structures, but the methods which have been developed in the study of anatomy are in every-day use by the pathologist in his researches. Especially useful are the histological and microscopical methods. Processes of imbedding, sectioning, and staining are absolutely necessary to the study of pathology.

Cytology is another very useful branch of botany to the pathologist. The finer studies in parasitism are possible only through a knowledge of normal cytology and through the use of cytological methods of research. Very little in fact has yet been done in cytological pathology, but this is surely one of the most promising lines for the future.

Plant ecology also lends aid to the pathologist. Disease in plant life may be defined as a condition of the plant by which it is partially or wholly incapable of responding to its environment. However, plants may be sickened by poisonous substances in the soil, may be injured by extremes of heat and cold, or injuriously affected by other environmental conditions so that disease results. After these unfavorable conditions have passed away, the plants are not prepared to respond to normal conditions. The ecologist understands the effect of environment on plants, their adaptations and struggles in competition with other plants and with unfavorable environment. When the plant succumbs wholly or partially in this struggle it becomes a pathological subject. Here ecology blends into pathology.

Bacteriology, although somewhat allied to mycology, deserves special mention as an aid in the study of plant diseases. A considerable number of plant diseases — no one knows how many as yet — are caused directly by parasitic bacteria. The study of these bacterial diseases forms in itself a very important department of vegetable pathology, and has enabled us to understand with considerable clearness a very large group of plant diseases. The usefulness of bacteriology is, however, still wider than this. The special methods developed in bacteriological research have quite revolutionized the life-history studies of fungi. I refer especially to the use of artificial culture media and the methods of isolating, cultivating, and inoculating parasitic germs. By these processes results which were only possible by the most laborious and uncertain methods thirty years ago can now be accomplished with the greatest facility by a student of only a few months' training.

Zoölogy, the sister science of botany, has contributed along many lines to botany, and therefore to pathology. Animal physiology, anatomy, and cytology have been extremely helpful. Many of the methods of sectioning and staining, especially the finer cytological and embryological methods, have been first worked out on animal tissues.

Entomology is connected with plant pathology in many ways. While the study of insects is itself quite distinct from the study of fungi, yet not infrequently the plant diseases produced by these diverse agents are difficult to distinguish till properly studied. The pathologist must know a good deal about insect injuries and diseases to distinguish them readily from fungus troubles. Furthermore, insects are largely concerned in the distribution of bacteria and the spores of fungi, and are thus important agents of infection. In the treatment by spraying in many cases an insect pest and fungus disease are killed at the same application. For example, the lime sulphur salt spray on dormant peach-trees kills the curl-leaf fungus and the San José scale. Bordeaux Mixture with Paris green or arsenate of lead kills the apple-scab and the coddling moth.

The utilization of physiological botany, the methods of staining, botanical microchemistry, as well as the studies of fungicides, bring the science of chemistry into continual use in pathological work. In fact, the limitations of the working bacteriologist and pathologist of to-day are largely in knowledge of chemistry. Most pathologists acknowledge that they have too little training in chemistry for the best results. The knowledge of theoretical chemistry, especially organic chemistry, is imperatively demanded in the further advancement of plant disease investigation. Perhaps no branch of natural science is of more use to pathologists at the present stage than physiological chemistry. It is opening the doors to entirely new fields of investigation in plant diseases. The general methods of research and laboratory equipment of the chemist are in frequent use by the pathologist.

A knowledge of physics is also of the utmost use to the working pathologist. While he can scarcely be expected to make investigations in the physical composition of soils, yet he must be prepared to utilize and understand the results obtained by workers in that line. We now know with more certainty than ever that many of the physiological processes in plant life are directly attributable to physical laws.

The plant pathologist should also have a general knowledge of horticulture and agriculture, or at least agronomy. He should understand the cultivation of plants, and should be prepared to master quickly and thoroughly the culture of any specific plant when occasion demands.

I have attempted to show that, while vegetable pathology is a somewhat narrow specialty, it requires very broad training on the part of the investigator. An ideal pathologist should have a thorough knowledge of systematic botany, including mycology, of physiological and anatomical botany, of cytology, ecology, and bacteriology, as well as a knowledge of zoölogy, entomology, chemistry, and physics, and allied sciences. I need scarcely mention that he should also have a good preparation in the languages, especially German, French, Italian, and Latin, and in such incidentals as drawing, photography, photomycrography, etc. A knowledge of horticulture and agronomy becomes absolutely essential when he starts in field work. Such a pathologist, of course, scarcely exists. Such complete equipment is hardly to be expected in one individual. No one realizes their deficiency more than the pathological workers themselves.

The Treatment of Plant Diseases

The object of an investigation of a plant disease is to find out the cause and remedy. If it is a parasitic disease the nature and life-history of the parasite must be determined. Its complete life-history is frequently necessary for full knowledge of the disease. The different stages of the organism must be worked out, where it spends the winter, how it reinfects the host plant, the climatic and other conditions which favor or retard its development or its parasitism. The stage at which it is most vulnerable, as well as the means of reaching and killing it, must be found out. If it is a non-parasitic disease, the causes or conditions which produce it are often still more difficult to ascertain, and the method of removing them or circumventing them is to be discovered.

The treatment for plant diseases is yet in its infancy, but successful results have been reached in many specific instances and along several lines more or less distinct. These may be classified as follows: (1) spraying with fungicides; (2) disinfection by means of germicides and fungicides; (3) eradication methods; (4) breeding resistant or immune varieties of the host plant; (5) cultural methods.

Spraying. The discovery of Bordeaux Mixture by Millardet about 1885 proved the starting of an important and successful era in the treatment of plant diseases. Spraying has probably accomplished more good up to the present time than any other method, or perhaps than all other methods together. The success of Bordeaux Mixture led to extensive studies of the other compounds of copper, some of which promised for a time to supersede the original preparation. While for certain uses copper acetate, and especially the ammoniacal solution of copper carbonate, have proved to be the best form of copper, yet the Bordeaux Mixture remains by far the most important fungicide. The sulphur compounds, whose use antedates that of copper, have also retained their place in the list of fungicides. The lime sulphur salt or the lime and sulphur mixture, on account of its usefulness in killing at one application certain fungi as well as scale and other insects, has become the greatest spray for dormant trees. During the last year or two dust-spraying, or, more properly speaking, dusting of plants, has come into prominence. The object here is to avoid the carrying and applying of large quantities of water, and instead to prepare the fungicide in a dust form, so that it can be thrown on the plant more economically. Rain or dew is expected to supply the necessary water to dissolve and more thoroughly distribute the fungicide over the plant. It has proved more satisfactory in the prevention of the coddling moth and leaf-eating insects, in the application of insecticides, than it has in the prevention of the fungus diseases. These are more difficult to prevent, and in many cases even too difficult to prevent by the finest sprays, so that the results in dusting are not thoroughly satisfactory.

Bordeaux Mixture has achieved notable triumphs in the prevention of the black rot and the *Peronospora* of the grape, apple-scab and pear-scab, pear leaf-blight on the pear and quince, leaf-blight of the plum and cherry, and the mildew and leaf-blight of the potato. Many other diseases are capable of prevention by spraying with this valuable fungicide. Curl-leaf of the peach is preventable by spraying with Bordeaux Mixture or the simple solution of copper sulphate shortly before the buds swell in early spring. The lime sulphur mixture is about equally successful applied at the same time. There are still some troublesome problems in the application of Bordeaux Mixture and other fungicides to growing plants. For some unexplainable cause, under certain climatic conditions, apples and pears are russeted or even deformed by the absorption of the poisonous copper through the cuticle. How to prevent this and to make Bordeaux Mixture that will be uniformly safe in spraying these fruits is an unsolved problem. Peaches and Japanese plums when sprayed in foliage, with Bordeaux Mixture or any other fungicide which has been tried, will, under most conditions, suffer severely. In most cases the fungicide kills round spots, which drop out of the leaves, producing a shot-hole effect, and at various intervals, from a few days to a month or two, all leaves touched by the fungicide fall to the ground. This defoliation results, of course, injuriously to the growth of the tree and the fruit. How to find a fungicide that will prevent the brown rot of the peach and plum and not injure the foliage is one of our most serious problems.

Disinfection methods. Certain diseases of plants are carried over mainly by means of spores or mycelium of the fungus which cling to seeds, tubers, and cuttings, etc. Where these can be disinfected and all the parasites destroyed, successful crops can frequently be grown in infested localities. One of the first treatments of this type was the dipping of wheat infested with smut in a solution of copper sulphate. Jensen found that hot water could be used for the loose smut of oats and other smuts successfully. The germination of the seed was even benefited by the treatment. Recently formalin has come into use for the same purpose, at first by the expensive method of dipping, and later by simply sprinkling it over the grain. Potato-scab was found by Arthur and Bolley to be preventable by dipping in a weak solution of mercuric chloride. Later they substituted formalin as a preferable disinfectant. The black rot of the sweet potato is preventable to a large extent by keeping the houses and hotbeds annually disinfected with copper solutions or formalin, and by selecting for planting only the sound tubers free from disease.

Eradication. No more puzzling disease as to its cause exists than the so-called "yellows" of the peach. There are two other serious diseases of the peach and plum of a somewhat similar nature, namely, the peach rosette of the Southern States, and the "little peach" of New York and Michigan. We are thus justified from their similarity in calling this type of disease the "Yellows Group." Peach yellows has been demonstrated repeatedly to be readily controllable by promptly digging up the diseased trees and burning them as soon as they appear in the orchards. Thus, while the yellows is one of the most obscure diseases as to its cause, it is one of the cheapest diseases to control. A careful inspection of the orchard two or three times during the season, especially at the ripening of the fruit, and the digging out of an occasional tree for the benefit of the rest of the orchard, is vastly cheaper than the thorough and repeated sprayings necessary to prevent the average fungus disease. Rosette is pretty certainly preventable by the same means. The writer is now engaged, with his assistants, in testing the feasibility of this treatment for the "little peach," with every prospect of success.

Pear-blight, the bacterial disease which attacks the blossoms, young shoots, and the bark of pomaceous fruit-trees, can be remedied, or rather prevented, only by the eradication method. It is more quickly contagious than the "Yellows Group" diseases, and the eradication is more laborious and difficult and not quite so successful. Black knot of the plum may be mentioned as another fungus disease which can be controlled by the eradication method. Simply cutting out the infected limbs in the fall or winter has been demonstrated to control the disease. Even some of the leaf-spot diseases, such as the leaf-spot of the violet, can be controlled by picking all the infected leaves as soon as they appear.

Breeding resistant varieties. Until recently our object has been to discover some method of spraying or disinfecting the diseased plants, or by destroying and thus losing them in the fight against disease. At best all these methods are somewhat extravagant and wasteful. By breeding varieties of plants which are immune to disease, or which are resistant to a greater or less degree, we may even avoid the necessity of treating the disease. No more desirable method can be imagined of getting around a troublesome plant disease. In fact, in cases of some root diseases, there may be no possibility of using the other methods. For an example, Orton, in his work on the root-rot of the cotton and cowpea, found resistant varieties which would not take the disease, and grew a fine crop on infested soil where common varieties were entirely destroyed. Swingle and Webber found that by the use of the sour orange as a stock on which to bud oranges, they were able to grow trees resistant to the root-rot of the orange. Webber found that the Drake Star orange was resistant to the *Phytoptus* rust on the orange. Bolley is breeding varieties of flax resistant to the flax *Fusarium* disease. In case of tobacco the mosaic disease appears to be susceptible of circumvention by selecting the plants free from the trouble. Mr. A. D. Shamel has achieved a notable triumph in selecting tobacco in the root-rot districts of Connecticut and Florida. Carleton, by breeding and selection, and by the introduction of resistant varieties of wheat from Russia and other parts of the world, has made excellent progress in growing wheat free from the rust. In this case, it would not pay to spray the wheat-fields, even if it were possible; so about the only way to avoid the losses from this disease is by growing resistant wheat. Of course resistance to a disease of parasitic nature is only one phase of plant breeding and selection. General vigor, ability to withstand unfavorable climatic conditions, productiveness, and special adaptability to certain soils and climates, or else wide range of adaptability are parts of the object of the plant-breeder.

This brings us to the fifth and last method of controlling disease.

Cultural methods. Every grower of plants finds that with most diseases, if he can grow strong, vigorous plants, they will be either immune to the disease or they will suffer so slightly from it as to grow successfully in spite of the trouble. By selecting proper soil and other environmental conditions for exacting plants, by the intelligent use of fertilizers and manures, the cultivator is able frequently to grow his crops with but little loss from disease.

In the arid regions of the United States the irrigated orchards and vineyards are almost entirely free from the fungus diseases of humid sections, such as black-rot and mildew of the grape, apple- and pear-scab, bitter-rot of the apple, and the ordinary leaf-spots. In Virginia the Newtown Pippin, when grown on the black, mountain loam soils, on the higher slopes and coves of the Blue Ridge Mountains, is nearly free from apple-scab and the fly-speck and smut fungus. It is also partly immune to the bitter-rot fungus. In low situations, or on the red clay hills at the foot of the Blue Ridge, it is extremely susceptible to all these troubles, so much so as to be commercially a failure there.

The selection of proper soils and localities for the peach, apple, and pear is a matter of the utmost importance in the commercial production of these fruits. This is true, of course, also of most of our garden vegetables and other crops. By the use of fertilizers we can frequently push plants into greater growth so as to enable them to resist partly or wholly certain types of diseases. Peach-trees infested by the root-rot, if heavily fertilized, will live and bear profitably without any indication of the presence of the disease. This is especially true in the Lake region, where the root-rot is apparently slower in its action than in the Southern States. The effect of fertilizers and stable manures is even more prominent in case of certain insect troubles than with the fungus diseases. A young peach-tree may be so sick from the attacks of the black peach aphis on the roots as to have every leaf rolled up and yellowed by the disease, and yet a bushel of stable manure placed around the tree in the winter and incorporated with the soil in the spring may push it into a vigorous growth the following summer, so that no trace of the symptoms can be noticed.

The study of root parasites gives us an additional reason for the rotation of crops. In fact, judicious rotation of crops is one of the best methods of shaking off and avoiding certain diseases. Nursery stock of the peach, when grown in an old peach location where a nursery or orchard has previously been located, will usually be seriously affected with root troubles, such as crown-gall, root-rot, and other fungus root parasites, eel worms or *Heterodera*, not to mention root aphis and other insect troubles. This can be nearly all avoided by growing the trees on a clean piece of land which has never been in peaches.

The application of lime to the soil has proved very beneficial in preventing the club-root of the cabbage and allied plants.

It should be noticed in this connection that not all diseases are preventable by high culture. Certain diseases on fruit-trees, such as pear-blight and apple-scab, more readily attack vigorous, well-fed trees than they do those growing moderately. Brown rot of the peach attacks trees with large heavy foliage on rich soil, or where an excess of nitrogenous fertilizer has been used, more seriously than it does less thrifty trees. It is necessary, therefore, for the cultivator to understand his particular plant as to its requirements and as to its diseases. No one has to know plants so intimately as the pathologist.

The early successes in the treatment of plant diseases have led to vigorous prosecution of this work by the Government. The section of Vegetable Pathology, of the Department of Agriculture, was organized in 1886, by one investigator. In 1888 there were four working pathologists. In 1893 there were nine. During the present season there are about one hundred investigators employed in the Vegetable Pathological and Physiological Investigations of the Department, the majority of whom are now in the field studying the diseases of plants. Considerable progress has been made by other governments, notably France and Germany. Nearly every prominent experiment station in the world has a plant pathologist on its staff. Our own state experiment stations have at work in nearly every state in the Union from one to five investigators. In Australia, in the Philippines, in Java, in Japan, and, in fact, in nearly every country where scientific botany is being pursued, contributions to the knowledge of plant diseases are being made.

SECTION E — ECOLOGY

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(*Hall* 7, *September* 23, 3 *p. m.*)

SPEAKERS: PROFESSOR OSCAR DRUDE, Kön. Technische Hochschule.
PROFESSOR BENJAMIN ROBINSON, Harvard University.
SECRETARY: PROFESSOR F. E. CLEMENTS, University of Nebraska.

THE POSITION OF ECOLOGY IN MODERN SCIENCE

BY OSCAR DRUDE

(*Translated from the German by Miss Jane Patten, Boston, Mass.*)

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IF, at a Congress fifteen years ago, ecology had been spoken of as a branch of natural science, the equal in importance of plant morphology and physiology, no one would have understood the term. That to-day in St. Louis it is given this rank is due to the zeal with which new lines of scientific research, inspired by discoveries in the most widely separated fields, have been followed during the last ten years; and no country has been in advance of America in placing in their true light the versatility, lofty aims, and scientific depth of ecology. In this country the floras of Minnesota, Illinois, Pennsylvania, and Missouri, also those including the region from the Appalachian Mountains and the Western territories to New Brunswick and Nova Scotia, have attempted to show how their contents are to be regarded by the light of ecology.

This new tendency has not arisen from any chance discovery; just as in the case of the study of bacteria, instruments had to be perfected before it could be placed upon a firm foundation.

In reality, this branch of science dates from the earliest period of botanical investigation, for in addition to the formal descriptions of those early times are found traces of a refreshing, vitalizing insight which connect mere description of the living form with the vital phenomena of the animate world.

Individuality and independence, however, had first to be woven from the weakest as well as the strongest threads which unite the "sciences of the earth," essentially geographical in substance, with the vital phenomena of the plant and animal kingdoms.

Physiology had taught how, with the aid of physics and chemistry, experiments could be made in the laboratory; it was obvious that these experiments could be repeated out of doors, where the changing play of nature's forces could be observed and fresh data obtained, which later could serve as a basis for further experiments in the laboratory.

At the same time this new tendency took strict account of the morphological development of those organs which, independently, according to their adaptation to the environment, determine to what biological form a plant or animal belongs. The ability of a plant to perpetuate its existence as a tree with deciduous or evergreen leaves, as a perennial whose powers of rejuvenation have endured for centuries, as a weed dying after the quick ripening of its seed, or else as a freely swimming or submerged water-plant, or a plant exposed to the stress of storms and winds, is just as important from the ecological standpoint as are the various means of locomotion developed by animals for the purpose of securing nourishment, such as springing, running, creeping, fluttering, and flying through the air, or wriggling through the dark earth, swimming freely on the surface of the water, diving in its shallows, — or else banished for life to the depths of the ocean.

We find the greatest variation in vital conditions in passing from pole to pole, from the ocean to the ice and snow of the mountain peaks, from the sun-scorched desert to woody and shady valleys, or to the cool caves hidden in the cliffs where is seen the greenish glimmer of the *Schistostega*. For each change in the vital conditions we find specially adapted forms of animal and plant life, and in the fundamental principles of animal and plant geography we find the earnest endeavor to contrast the more physiographical details of distribution with the dependence of the adapted form upon the environment; this latter, with its great biological importance, being more especially the province of the zoölogist and botanist.

In this manner has the study of ecology come into being, and, since it has been most clearly and easily followed in botany, the word in its modern meaning has come to denote more especially the ecology of plants. Therefore the honor to address this Congress upon the subject of ecology has been given to a botanist, who is a plant geographer as well.

By the word "ecology" we understand the vital phenomena exhibited by plants and animals in the struggle for space, under conditions enforced by the climate and the physiography of a country. "Struggle for space" is Ratzel's appropriate version of Darwin's proverbial phrase, "struggle for existence," whose purport, however, remains unchanged. In the struggle for space each organism requires a place in which he can fulfill his career; that is, secure nourishment, and leave behind him descendants capable of occupying a similar location. Each organism is closely associated with its environment; each plant, each animal, lives, like mankind, in a special world of its own.

These considerations show us that ecology is the borderland to which the sciences of biology and geography can both lay claim. Thus the ecologist, persuaded of the importance of the various vital problems which here cover common ground, must have a complicated equipment for his varied work; he must be as familiar with the use of the balance, photometric and thermometric instruments, as with the absolute dominion of lifeless nature. In order not to be betrayed into forming hasty conclusions, he must work in the herbarium as a florist, with the microscope as a physiological anatomist, and also bear constantly in mind the geological development of present conditions.

Yet until now botany and zoölogy have held aloof from one another in this new scientific departure, although it is just here that victories common to both have been achieved,—as, for instance, in the biology of the flower whose form shows adaptation to the needs of the insect world; or in cases where there is mutual dependence between plant and animal, the one affording domicile, the other protection, as in the case of the Imbauba trees of Brazil, which furnish food and lodging to armies of ants, who in turn protect the trees from the devastating hordes of leaf-cutting ants. In this connection, too, has been brought to light the usefulness of the modest earth-worm and the versatility shown by plants in the methods used for protection from the voracious assaults of snails and caterpillars. The dire need of animals struggling to obtain their scanty nourishment is often revealed at the same time as the silent efficacy of the protective forces of the plant kingdom.

We can readily understand how through all ages the effect of large troops of Herbivora has been harmful to the plant world, while the effect of their enemies, the Carnivora, has been beneficial, and how these two influences must have produced various changes in the formations.

In determining the dependence of organic life upon the physiographic character of a country, the science of botany is naturally of the utmost importance, since the individual plant is found actually connected with the outer world. Animals that live alone, or are banded together in flocks, swarms, or herds of the same species, are naturally incapable of building formations dependent upon the climate and inseparable from the soil. Their power of locomotion is a hindrance to the close connection with Mother Earth that is maintained by the flora.

Ecology is new in name only, and while stress has lately been laid upon the versatility of its special methods, we find the sources from which they have been derived far back in the past century, and the connection between ecology and geography, as evidenced by the restriction of the animate world to stations with special physiographic features, is expressed in the excellent floras of earlier days. Linnæus, in his *Flora lapponica,* a work which until recently has hardly received due recognition, has given us an example of how a flora may not only give a diagnosis of the different species, but also a description of their mode of life. A flora containing a description of the methods employed by the most widely distributed plants in perpetuating their existence, unfolding their blossoms, and ripening their seeds, is of the utmost importance for the true comprehension of the part played by every species in covering the soil with verdure. The worthy florists of that early period undoubtedly recognized the fact that the appearance of similar associations followed definite laws which they endeavored to express in the terminology used in their diagnosis of the situation; thus they actually were the founders of the modern doctrine of "plant formations."

But in order that ecology should advance to the rank of an independent branch of science capable of further development, the creative genius of an investigator was needed, who, unsatisfied by the older methods of description, could work from a more general basis. During his long journeys through distant lands, Alex. von Humboldt had recognized the special scientific value of the mutual relations existing between the annual change of season and the form of vegetation assumed by predominating plants. Accordingly, he chose a few representative orders of the plant kingdom, fifteen in number, such as palms, conifers, cacti, tree-ferns, mosses, and lichens, which by their mode of growth and perennation give a certain definite physiognomy to the district in which they predominate, since each one of these groups gives rise to landscapes totally differing in character. Von Humboldt was undoubtedly guided by the ecological spirit, as we should say to-day, in the elaboration of his excellent system, whose defects lay in the then existing confusion of vegetative form with systematic character.

Alphonse de Candolle enumerated these defects, when, in his *Géographie botanique raisonnée,* he laid the foundation upon which could be based the study of a flora from the evolutionary point of view, and confined climatological considerations within their proper limits. But A. Grisebach in his earlier works had already begun to develop the doctrine that the victories of the all-conquering climatological factors find their outward expression in "formations" composed of special forms of the vegetation with which our earth is decked. The cactus alone does not determine the arid character of the desert, nor the Mauritia palm the tropical character of the Amazon region, nor the Lodoicea that of the Seychelles Islands. Mosses and lichens are not the only plant growth on the Siberian and Canadian tundras; and among the conifers the northern larches bear witness to quite different ecological conditions from those designated by the cedars of Lebanon, or the Araucarias which grow in eastern Australia and on the southern shores of the American tropics. With these plants, however, grow other species having the same requirements in regard to light, heat, and moisture, and all these together make up a typical formation in their common station.

Since Grisebach elaborated these fundamental ideas and gave them general expression in his *Vegetation der Erde* (1872), he may be regarded as the founder of the third period in the development of ecology, just as I regard von Humboldt, with his *Essai sur la géographie des plantes*, to be the founder of the second and Linnæus that of the first, which began with the appearance of his *Flora lapponica*.

As yet, however, the ability to penetrate the intimate relations existing between climate and plant life was lacking. The discovery of mere outward facts of contiguity furnished only the barest outline, which still needed the accumulation of important data for its true comprehension.

Knowledge of the evolution of the earth and of organic species became the aim of scientific research. Darwin's great intellectual achievements bore universal fruit. Such men as Moritz Wagner attempted to extend questions of theoretical evolution so as to include the problem of the distribution of species, until then regarded as something fixed and unalterable, and thus the idea of evolution became involved in the explanation of present conditions. In a similar attempt, especially in botany, to give formal diagnosis a more natural bent, the mere description of organs was transformed to biological morphology, while anatomy was changed to physiological anatomy. For floristic purposes the attempt was made, by means of the clear and simple methods used originally in experimental physiology, to correlate organs with the physiological factors of the environment.

While these new tendencies, developed from morphology and physiology, which to-day form the closest connection between the organic and the inorganic worlds, were advancing and the vast amount of material already collected was being worked over, a special branch of science had arisen, namely, the biology of the flower, which, instigated by Darwin's work upon the mutual relations existing between different organisms, set aside the ancient opinion that zoölogy and botany could proceed side by side with absolute disregard of their dependence upon one another.

The pivot upon which investigations concerning the pollination of flowering plants turned was the "law of avoidance of self-fertilization." Facts which to-day are universally taught in the schools still remained to be proved by such men as Darwin, Hildebrandt, Hermann Müller, and others. It was discovered with astonishment that Koelreuter toward the middle of the eighteenth century, and K. Sprengel in 1793, had already disclosed "the secret of Nature in the structure and fertilization of flowers." Until then, however, no one had applied the biological relation between flowers, wind, and the insect world, as shown in the phenomena of pollination, important enough to be included in the science of botany, nor had any one made clear the mutual dependence of the animal and plant kingdoms in their household economy. These factors in the struggle for existence were now given their full value, and the different appearance of various associations was explained by the absence of this or that insect, while in tracing the boundaries which limit the area of distribution of certain plants and animals, as, for instance, *Aconitium* and *Bombus*, the organisms were found by Kronfeld to be interdependent.

Thus in the fourth period of the development of ecology, widely separated branches of science are brought together in order to explain the life-history of a certain region. These, however, must be united in the realm of geography to form a new entity, and, by their correlation of numerous data, prove the propriety of their use. The evolutionary tendency, which extends far back into the geological past, and is based upon knowledge of the areas of distribution of hosts of related genera and species, has been considered, especially in botanical geography, as a subject quite separate from that which treats of the vegetative forms and the formations as physiological entities, dependent upon external factors.

The division of entire continents into zones, as seen in the atlases of physical geography, gave expression to this feeling. It was also necessary to extend the ecological method to the field covered by the publication of special floras, and with renewed interest and zeal to begin the revision of the enormous mass of material collected therein. This work had already been begun in the floras of central Europe, which were soon followed by the excellent departmental work of the North American Surveys. Occasional brilliant descriptions of tropical floras, such as the descriptions of the vegetation of Lagoa Santa, in Brazil, also that of Juan Fernandez and the division of Mt. Kinabalu, in Borneo, into regions, quickly bore the methods of the doctrine of formations to distant lands, whose floras until then had only been known to us through the systematic enumeration of their orders. Thus the way was prepared for the recognition of ecology as a new and special centre, and scarcely ten years have elapsed since this centre, which would unite biology to the natural sciences, was demanded.

Whoever wished to pursue the study of the physiology and development of organs, in order to understand the weapons used in the struggle for space on land or in water; whoever wished to study the mutual relations of species, rather than their inherited characteristics, or to consider the flora and fauna not only as they determine the characteristic appearance of the country they inhabit, but also as being the external, vital result of the effect of geographical factors, which is capable in its turn of influencing the aspect of nature, had to be called an ecologist, whether he wished to be so designated or not. Even the name of this new branch of science was still in dispute and no one was satisfied. To-day, however, we need not concern ourselves with the name. From the beginning, the mutual relations existing between the various branches of science exerted upon ecology the powerful influence which usually only accompanies the gradual change from the purely scientific to the utilitarian point of view.

In this historical sketch we have now reached the fifth period, which begins with the publication of MacMillan's well-known study of the *Lake of the Woods* (1897) and Warming's *Lehrbuch der ökologischen Pflanzengeographie*. These works emphasize the special province of ecology and give preference to the methods employed in the organic natural sciences rather than to those used in the geographical. It soon appeared as if this daughter of bio-geography would destroy the reputation of her mother and usurp her place, but the opportune appearance of Schimper's work, based upon the same foundation and fulfilling Grisebach's unattainable dream, completely restored the connection between the highly specialized ecological and the broader geographical points of view. The most distinguishing characteristic of this last period, however, is the closer bond of union established between ecology and phylogeny.

Evolutionary thought, which is the keynote of modern natural science, may proceed along two lines: according to the variation of species in regard to their spatial requirements, or according to the variation of an association under the influence of successive generations, each of which has undergone modifications. In this way the study of phylogeny is extended to the field of floristic geography. The connection between these two lines of thought will be readily seen, if we consider certain recently evolved, feeble endemic species in connection with their nearest relatives, and also study the history of their modification under the influences of time and external circumstances. As such species we may mention the glacier willows of Nova Zembla and the twenty-three species of the genus Hieracium, restricted to the Faroe Islands and described by Dahlstedt. The presence of such species gives a decided geographical character to the region in which they occur.

Under the title *Géographie botanique expérimentale,* Bonnier endeavors to prove the direct effect of change of climate upon the variability of specific forms, and Géneau de Lamarlière uses the phrase *physiologie spécifique* to express the idea of the degree of adaptation accomplished. R. von Wettstein draws his conclusions from different premises, since he considers that the species which have been developed have been derived from related species and from those closely restricted to the same location. Having made this assumption, he then proceeds to search for the causes which have been influential in the accomplishing this end.

The ecological point of view includes those things concerning the question of continuance in a given location, the power of obtaining nourishment, and the certainty of establishing the succession, which are not general and uniform, but which differ according to the varying factors of the environment. Ecology is the study of epharmony in the organic world, and the possibility of variation possessed by species, as well as the mere fact of their life together, is an ever-present, dynamical factor in the determination of the external appearance of our earth. But it is not enough simply to discover and describe these various specific relations; we must press forward and from the mass of accumulated data obtain an intimate comprehension of the organic form in its dependence upon Mother Earth!

During the course of our historical sketch of the development of the ecological idea, three special points of view have been made manifest, namely:

(1) The relation of the organization of ecological forms to the morphology of plants and animals (morphological relation).

(2) The relation of the ecological formation to the physiography of the country (physiographical relation).

(3) The relation of ecological epharmony to the phylogeny of systematic groups in both animal and plant kingdoms (phylogenetic relation).

If we wish ecology to rank as a special branch of biology, we must undoubtedly consider these three points of view as inseparable, and we may give our attention to either one or the other, just as, until recently, most North American studies have been devoted to investigation of the ecological station and the analysis of the smallest associations. The union of the morphological, geographical, and phylogenetic points of view upon the physiological basis of adaptation and dependence, alone gives us the essence of ecology. Therefore we will devote the following remarks to an elucidation of these three fundamental ideas, and try to show how intimately their connecting threads are interwoven.

(1) Considering the many internal and external differences in the adaptation of various organs to the environment shown by aquatic, rock-living, forest, and swamp plants, or springing, flying, creeping, and swimming animals, it has been thought expedient to elaborate this point of view separately, which serves as a basis for physiological anatomy. The works of Schwendener, Vesque, and Haberlandt, which turned the methods of systematic, anatomical description into physiological channels, gave botany its freedom. Yet it is difficult to develop a special ecological system of instruction from morphology and anatomy alone, since an inextricable network is formed by the relations existing between inherited systematic structure, climatic factors, regional peculiarities, and the influence of coexisting plants and animals, whether friends or foes.

Each one of these relations is capable of forming a basis for comparative analysis and classification. The dissatisfaction felt with earlier as well as with more recent divisions, such as those given in Reiter's *Consolidation der Physiognomik* (1885), is explained by the inconsistencies which necessarily attend the incessant change from morphological to physiological or physiographical characteristics, and it is doubtful whether we shall ever be able entirely to avoid them. The difficulties are most apparent when we attempt to change the accustomed systematic arrangement of our museums to one which shall represent the ecological features of a given formation. It is, however, necessary to work out this new point of view, using ecological types as a basis.

There are quite a number of individual morphological forms having no definite ecological meaning; undershrubs, shrubs, and bulbs are found distributed in the most dissimilar stations in every clime, while their requirements in regard to season, warmth, and light differ totally. Undoubtedly the most important forms of vegetation are those which depend directly upon the climate and whose appearance typifies to the geographer, unversed in ecological methods, a certain definite landscape. Von Humboldt tried to do justice to the importance of these forms when he made the first attempt at classification.

The principles of ecology have been of especial value in the introduction of ecological names, which refer to annual periodicity, such as "evergreen leather-leaf plants," "trees bearing a tufted, evergreen crown," and "leafless, perennial succulents," in place of the systematic names of orders whose predominance characterizes a given landscape, such as conifers, palms, and cacti. The leaves have come to be more and more regarded as a distinguishing characteristic, and to them is dedicated Hansgirg's *Phyllobiologie*, in which they are classified according to their pubescence, their flexible or rigid character, or according to their structure for protection from light, wind, or rain, or the method they adopt for shedding water, either by means of "spouts," or of an impervious wax covering. It is their structure which bears the imprint of the climatic seal and determines the fundamental form of tree, shrub, bulb, and mat, just as their period of activity determines the length of the season. Thus in groups formed according to leaf and vegetative period, we naturally find the most diversified sub-groups, among which may be reckoned those classified according to the mode of displaying the flower, the manner in which it is fertilized, the protection of the pollen from rain, or the characteristics of parasitic or insectivorous plants, while there may still be others arranged according to the station, either in light or shade, on dry or moist soil, or humus or on rock.

As yet, science has not succeeded in obtaining a satisfactory enumeration of the separate ecological forms, for this, the science in its anatomical and physiological aspect is still too young, but it is a pleasure to see the increase in investigation along these lines and the severe criticism to which the results are subjected. For the future, we can predict a classification of living forms, which, based upon observation of external appearance, will appeal to a far larger circle than do the intricacies of phylogenetic research, whose embodiment in a system offers just as great difficulties to the more formal methods of classification.

(2) Ecology is the doctrine of reciprocal biological relations and of the adaptations acquired in the struggle for space and necessitated by the existing conditions of soil and climate; we may therefore consider that these terms show us the links by which ecology is indissolubly bound to the geographical sciences. Still, it would not be right to consider botanical geography as only the same matter as botanical ecology, since, taken by itself, and without due regard to the ecological interpretation of phenomena, there exists also an abstract, geographical method of considering the organic world.

If, however, we survey the organic world from the geographical point of view, it seems to us of the utmost importance to divide it into organic districts which will represent the essential characteristics of continents, islands, mid-ocean, and seacoast. From the biological point of view it seems of the utmost importance to discover the causes determining the different areas of distribution, by an investigation of the life-history of our present environment, or, when this fails to give the required explanation, find out, by patient research among the geological records of the past, the locations where analogous conditions must have prevailed.

The essence of geography is the endeavor to acquire knowledge of the distinctive features of the earth, and for this purpose all the data of related sciences must be collected. Since the organic sciences are constructed from separate bits of knowledge, they must take each fundamental element into account, that is, consider each individual species according to its inherent qualities and external form. The tendency of ecology to accumulate minor details obstructs the broad view towards which it has painfully toiled, until the introduction of the freer methods of geography aid it in uniting the results of divided effort. We have here before us an excellent example of the intimate connection between two branches of science, the one being the complement of the other and acting as a stimulus to further investigation.

The attempt has been made to introduce into ecology various phrases which shall have a definite, geographical application, but in order to do this, due justice has not been done to existing facts. The phrase recently used, "Climate creates a flora, soil determines the formation," seems to me to be unfavorable for the advancement of future research along those lines where climate and soil furnish a causal explanation.

Climatology especially must be restricted within its proper limits, where, however, it must be given all its privileges, as, for instance, in the classification of continental zones. It seems to me entirely wrong to allow the undue influence of a certain factor to establish unnatural scientific divisions in a subject whose inherent worth lies in the correlation of the most heterogeneous data. The defects which arise from the use of a single morphological characteristic have been recognized in systematic classification, so that here, where the investigator must deal especially with the complexity shown by determining factors, the giving prominence to one factor alone will enable him to illumine only a small portion of the field and will give him but imperfect means of taking his bearings.

In the determination of both large and small divisions the naturalist is ever haunted by the same questions: for which forms of vegetation, as well as for their union into formations, is each district best adapted, and by what vital conditions does it differ from neighboring districts?

It is strange that until now the ecological branch of animal geography has almost neglected this, to me, most interesting side of the question. Yet the periodic phenomena of animal life, so often contemporaneous with those of plant life, should invite the investigation of the naturalist. Recently, in the subtle work of Kobelt, animals have been divided into great groups according to their behavior toward the northern winter, as well as according to the cause and forms of their migrations. This immediately brings up questions as to the climatic limits of their distribution, the southern boundary of hibernation, and also of the parallel which separates the winter and summer quarters of the northern eider-duck from those of the Antarctic penguin which cannot fly. With these we may compare the shorter migrations of reindeer and bison.

The time may not be far distant when the geographical maps of the animal kingdom will emphasize this point of view more strongly than the fact of mere territorial distribution. For its part, botanical geography is occupied in making clear in separate, experimental works, the connection between landscape and formation, and, by imitating geology in the publication of special maps, a long-felt need is being satisfied. Such actual accomplishment counts much in a field where our wish to make clear the cause so far outstrips our ability to do so, for we must not forget that in all other special scientific branches the final aim lies before us much more clearly than in ecology, which must be regarded as a place of public assemblage, and it would fare but poorly if it spoke of a final aim before sufficient work had been accomplished in the investigation of all vital phenomena.

The difficulty of stating clearly the reasons for the changing garb of this or that formation is shown by the circumspection used in MacMillan's work upon the *Lake of the Woods*, where, for the first time in America, this attempt has been made. We find another expression of this difficulty in the rows of figures enumerated in Jaccard's comparison of analogous association in the mats of the Swiss Alps. The vital question here is: Why, when fruits and seeds are so widely disseminated, do the stations of the different species remain so clearly defined within the areas of distribution? Even if we could empirically determine the vital needs of a single species by a consideration of its climatic requirements, area of distribution, and nature of the station, we should still be unable to explain the inherent differences caused by a greater or less degree of acclimatization, or the changing association of species and their different bearing in widely separated districts.

(3) Thus we are led to a consideration of the essence of species, in whose powers of adaptation and variation we find the key to the important problems which weigh upon us when we regard the abundant forms of life which take part in the world's work and live in peace and harmony under the favorable and unfavorable influences to

which they are subjected. This last point of view is that of ecological phylogeny, or the study of the variability of species during the struggle for space under the direct influence of newly acquired qualities.

The accumulated data concerning isolated, endemic species and the nearly related forms of a large specific group distributed over an extensive area, are only seen in their true light when we observe the ecological requirements in connection with distinguishing systematic characteristics and also take into consideration the results of recent research concerning the variability of species. Thus we may study from an ecological standpoint the problem suggested by Jaccard as to the cause of the reduction in number of species inhabiting a limited area, the number of genera being correspondingly large. This fact has long been noticed on islands in mid-ocean, and comparison has shown it to be equally true for separate mountain ranges. It appears as if a natural genus, rich in species, were permeated by certain fundamental ecological qualities, which enable it to appear in many places as victor in the struggle for space, yet each species of this same genus can only appear in a few places, so that an association may consist of many different genera, but each genus will be represented by only a few species. This appears to be the solution of the problem concerning the development of representative species in widely separated districts whose floral elements appear to have had the same ancestry. This is shown by a comparison of the European, North American, and East Asiatic floras, where we so often find nearly related species filling a similar ecological rôle. The larch belonging to all three continents, many moorland shrubs, the beech and the birch, all having a wide distribution, can be cited as affording excellent examples of this fact. *Sorbus Americana* in the mountain regions of New England and New York holds a position similar to that of *Sorbus aucuparia* of central Europe. Few species have remained exactly the same; the greater number have been broken up into representative forms, showing on the one hand species with decidedly similar ecological adaptation, while on the other hand many species have developed into dissimilar forms possessing dissimilar modes of life.

The persistence of certain ecological habits in a species, genus, or family, is made the basis of paleontological conclusions. We judge of the climate of central Europe during the Miocene epoch by the conditions existing to-day in places where we find Taxodium, Sequoia, Sassafras, Magnolia, and Platanus. The beeches and firs of that time, we consider, were relegated to the mountainous districts. It seems to us hardly probable that a plant like Taxodium, which in the warm Miocene reached as far north as Spitzbergen and Greenland, and has remained unchanged in form for one hundred thousand years, should alter its climatic requirements; we feel rather that it persists to-day only in those places where the hypothetical Tertiary climate still predominates.

If we need still further illustration, we might mention the fact that agriculture, developed through centuries of human experience, is a branch of ecology which long preceded methodical science. In agriculture man took the household economy of plants into his own hands in order to provide them with the necessary light, the most propitious time for germination and ripening of the seed, and the most suitable soil, paying due regard, however, to the succession of seasons peculiar to the country and to the meteorological conditions.

A botanical garden to-day, richly equipped with natural plantations of every kind, greenhouses, moist and dry, hot or warm, bright, or illumined by cool, green light, shows how many plants, native to all climates and having the most varied requirements, may actually be brought together in a small space by means of the careful imitation of those conditions which we observe in the immense extent of territory stretching from equator to pole. Progress in horticulture denotes a minute observance of the vital phenomena of all the plants we wish to assemble about us, and physiological investigation of the effect of temperature and season give us the knowledge necessary to change winter to spring in our drawing-rooms and conservatories.

Humanity gladly claims its share of the achievements which beautify existence. Universal cultivation of the intellect cannot remain unaffected by results, which, together with those of other branches of natural science, escape from their special field to become so widely disseminated as to fill the thoughts of man and counterbalance the effect of the strictly logical, mathematical point of view.

Ecology has arisen from the need to unite originally separate branches of science in a new and natural doctrine; it is characterized by the breadth of its aims, and its peculiar power and strength lie in its ability to unite knowledge of organic life with knowledge of its home, our earth. It assumes the solution of that most difficult as well as most fascinating problem which occupies the minds of philosophers and theologians alike, namely, the life-history of the plant and animal worlds under the influences of space and time.

THE PROBLEMS OF ECOLOGY

BY BENJAMIN LINCOLN ROBINSON

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One hundred years ago our country more than doubled its extent. At the anniversary of this great event, one of the most momentous in our national history, it is fitting that its widespread effects should be considered not merely in relation to the growth and material prosperity of our country, but to all phases of the intellectual and scientific development of the nation. Our subject this afternoon is certain problems regarding plant life, problems which have become practical, important, and even vital to the interests of the American people, largely through the very territorial accession which we are now commemorating. While the Louisiana Purchase doubled the area of the United States, it increased in a far higher degree the physical and climatic diversity of the country. The newly acquired territory contained wider prairies, higher mountains, greater forests, deeper gorges, and more arid plains than any east of the Mississippi. It was a region of extremes of altitude, temperature, and precipitation. Its successful exploration, settlement, and agricultural development presented to our government and national energy problems as intricate in their solution as they were vast in magnitude.

Furthermore, the subsequent annexation of Texas and California was a logical sequence of the Louisiana Purchase, for it would scarcely have occurred had Louisiana remained in foreign possession. When the great Southwestern and Pacific States, with their still more varied climate and floras, are thus brought also into consideration, it will be seen that the Louisiana Purchase has directly or indirectly increased by many times the extent and importance of the botanical problems of our nation.

It is a matter of common experience that one of the best indications of the value of wild land is furnished by its native vegetation; and it is of interest to notice how early in the exploration of the Louisiana Purchase this fact was realized. The management of this great and beautiful exposition has named this very day in honor of

Lewis and Clark, the first effective explorers of the original Louisiana. Every botanist may recall on this occasion with pleasure the fact that Captains Lewis and Clark gave much attention to the strange and varied vegetation of the regions traversed during their intrepid journey into the pathless wilderness, which will always form one of the most thrilling and dramatic incidents of our national history. What is more remarkable, they brought back with them a considerable number of plants. It is pathetic to think under what difficulties and with what devotion to science these plants were collected, prepared as scientific specimens, labeled, securely packed, and transported thousands of miles overland under circumstances which made each pound of baggage a source of untold labor and peril. It was through these specimens, so heroically obtained, that the floras of the vast and varied valleys of the Missouri and Upper Columbia first became known to science.

At the time of Lewis and Clark the study of plants had but two important branches. These were classification and economic botany. A plant was investigated solely with the objects, first of determining its place in a rather arbitrary system, and second of discovering its uses. At the beginning of the twentieth century, on the other hand, botany, now become one of the richest sciences in carefully observed and accurately recorded facts, is divided into many highly specialized fields of research. While the extent to which this subdivision has now been carried is often a surprise to the non-botanical, such terms as plant classification, plant anatomy, vegetable histology, physiology of plants, vegetable pathology, paleo-botany, and the like, are readily comprehensible to the intelligent layman. He may derive from them a considerable idea of the nature and importance of the subjects they designate, even though he may be ignorant of their extent and details. The word ecology, however, is too recent and technical in its application to be familiar to many who have not been professionally engaged in some phase of botanical work. The term, although equally applicable to plants and animals, has been used far more freely by botanists than zoölogists, and it is solely in its botanical sense that it is here employed. Of the various definitions of ecology I believe none surpasses in terseness and excellence that suggested by Professor Barnes. "Ecology is that portion of botanical science which treats of the relations of the plant to the forces and beings of the world about it."

The scope, significance, and probable future of ecology can only be understood after some examination of its origin and history. The subject, although older than its name, is still a relatively new one, and it is worth while to examine its position with regard to the older branches of botany. The relation of ecology to plant geography is especially complicated and difficult to state. Discussions on this subject are apt to leave the reader a little in doubt whether ecology is to be regarded as a phase or subdivision of plant geography, or whether plant geography is only a generalized form of ecology, or finally whether the two are capable of separation even by a rather vague boundary. So much, however, may be said with definiteness. These branches of botany have arisen independently and differed greatly in their history and point of view. They have both dealt with adaptation of plants to conditions of soil, climate, and communal life, but have approached the subject from opposite sides. Plant geography, much the older of the two subjects, was at first closely allied to systematic botany. It was pursued chiefly by systematists, and consisted largely of a series of generalizations upon the distribution of genera and species and their rough grouping into floras. More and more has the plant geographer studied the adaptive traits of plants, and observed their biological rather than their systematic relationships, until he now bases most of his conclusions upon ecological data. On the other hand, the ecologist, beginning with the individual plant and examining the relation of its structure to its activities and the activities to the environment, has been gradually and naturally led to wider and wider generalization regarding the influence of structure upon distribution and of environment upon structure, until in his plant societies and plant formations, he has speedily arrived by another path at just the point more slowly reached by the plant geographer.

The material of these two branches of botany is nearly or quite coextensive. It is difficult to find any ecological modification of a plant which is not at least in some slight way connected with its distribution, and conversely the present distribution of plant life, which forms the subject-matter of plant geography, has undoubtedly resulted immediately or remotely from ecological causes. It has been well said that plant geography is the study of the present consequences of past ecological conditions.

By its nature plant geography has been descriptive and classificatory. With all due regard to their natural affinities, adaptation, and gradual association, it has grouped plants primarily according to the soil and climatic conditions in which they grow. Ecology deals with the dynamics of plant life, with such phenomena as competition among plants, crowding and tension of floras, migration of plants, parasitism, symbiosis, and the complex relations of benefit and injury which exist between plants and animals. It is of all departments of botany the most recent in development, rapid in growth, and fascinating in subject-matter. The details of classification, anatomy, and physiology are dry and cold compared with such ecological discoveries as the varied modes in which plants are protected against the attacks of animals, the complicated ways in which they scatter their seeds, or the highly complex adaptations of their flowers to secure cross-pollination. What facts of systematic botany, for instance, can be compared in popular interest with the adaptations of the ant-plants or the marvelous biological relations of the Yucca flower and Pronuba moth so critically studied by a distinguished botanist of this city? Ecology presents plants in their most human aspect. It deals with their struggles for room, light, and food.

It would be natural to suppose that a subject so varied and fascinating would have been among the earliest phases of plant study to receive attention, but it is only within the last two decades that ecology has asserted itself as a department of botany. Of course, the observations and records upon which ecology rests have been accumulating for centuries. The task which has been accomplished in recent years is the arrangement of these observations in new sequences and their interpretation from a new point of view. It is scarcely necessary to say that the new standpoint was furnished by the theory of evolution.

This being true, however, it would be natural to ask why the effect was not more immediate, and why a quarter of a century elapsed between the clear enunciation of the Darwinian hypothesis and the first organized study of ecology. This was due chiefly to two causes. In the first place the Darwinian theory itself was, in its varied aspects, a matter so important, and so violently discussed in its early years, as to leave among speculative biologists little attention for other matters. On the other hand, mechanical improvements in the microscope, microtome, and other such apparatus had just then opened great vistas of technical research along the lines of plant anatomy and physiology, which consequently formed in the sixties, seventies, and eighties the most popular fields of botanical study. Here the spirit of investigation was by no means speculative. Anatomical structures were studied in great detail, but there was an almost morbid reluctance to theorize upon their physiological significance. In like manner the physiologist was measuring and weighing, timing and recording the vital processes of the plant, but his work was chiefly in the laboratory, and he was not given to speculating upon adaptations to environment or the complex influences which determine plant distribution. The plant physiology of the seventies was as far removed from ecology as human physiology is from sociology.

In the late eighties and early nineties a feeling arose almost simultaneously in several quarters that anatomy to be of real value should be physiologically interpreted, and that physiology should go forth from its laboratory to observe and name a host of processes and forces of nature, which are no less important because in many instances they can neither be measured nor weighed. The new science, thus called into existence, was first spoken of as biology of plants, but it was quickly found that the term biology, already overloaded with meanings, would prove but poorly distinctive in this application, and the name ecology was substituted.

It is easy to understand the rapid growth of the subject. The most attractive phenomena of nature were awaiting its reclassification. The speculative biologist had done much to clarify ideas upon the evolutionary history of the vegetable kingdom. The unspeculative histologist and physiologist had been accumulating a great wealth of facts, which were ready at hand to be correlated by broad and interesting generalizations. Systematic botany added its well-nigh boundless literature regarding the affinities and diagnostic features of plants. Conditions were all favorable.

One of the greatest difficulties of the ecologist has been to find a simple basis of classification for the phenomena covered by his subject. Their great diversity has made it hard to group them in a logical system. Their common element is too slight to suggest a consistent arrangement. It is true, ecology can in a very broad way be divided into the relations of plants to their inorganic environment, to other plants, and to animals; but this does not go far toward a satisfactory classification. The clearest and by all means the best basis for the grouping of ecological facts is their geographic aspect. As has been already mentioned, there are few if any ecological modifications of plants which cannot be in some way correlated with their habitat. It is in this way that ecology has now become inextricably merged into phytogeography, and that phytogeography enriched by ecological methods has become one of the most attractive and promising fields of botanical research.

Having thus endeavored to make clear the general nature and origin of ecology, together with its historical relation to phytogeography, I may proceed to their joint problems, treating henceforth the two subjects as coextensive and forming but a single discipline.

The examination of plant life from a new point of view necessitated to a great extent a new nomenclature. All ecological phenomena, and especially every phase of plant distribution, had to be reëxamined in a detail which could not be technically expressed by existing words. Old terms were redefined and new ones invented in bewildering succession. This nomenclature is still inchoate, for the growth of interest in ecology has been so sudden that there has been no time for its language to become fixed by usage or for any survival of the fittest to determine which of its many synonymous terms will prevail. There are at present two general practices or tendencies apparent. Many of the most critical and effective writers on plant relations have contented themselves with a small number of new terms. In expressing a novel idea for which no technical term was at hand, they have avoided coining one, and have used instead some descriptive phrase.

On the other hand, it has seemed desirable to some of the more strenuous, especially in America, to make up an extensive and highly elaborated vocabulary.

Neither of these practices should be hastily condemned. The former method of expression, even if seemingly less precise and erudite, has the great advantage of immediate clearness. It is businesslike, practical, and free from any suggestion of affectation or pedantry. But on the other hand, in favor of such an elaborate terminology as that suggested by Professor Clements, it may be forcibly urged that a well-chosen technical term, even for an obscure conception, not only makes for brevity, but does much to fix and clarify the idea. It gives a convenient handle to a thought which may be otherwise difficult to grasp and awkward to employ. It may be further argued that most branches of science are considerably incumbered by a faulty and often misleading nomenclature of casual and unsymmetrical growth, by no means ideal, yet too firmly fixed to permit of reform. Is it not, therefore, desirable that ecology, a new branch of science, should be supplied at once with an adequate and consistent terminology, and thereby be spared many wordy wranglings and abortive nomenclature reforms which must inevitably result from a *laissez faire* policy in this matter? It cannot be denied that this reasoning has weight. Surely there is no systematist who does not regret the lack of convention in this regard among early writers upon his own subject.

The first great problem of ecologists is, therefore, to establish an adequate, expressive, and logical language of their subject, — *to establish,* I repeat, not merely *to invent* such a terminology. If effective uniformity in methods of expression can be accomplished, it will well repay prolonged effort and do much to give precision as well as dignity to the subject. In just this matter of nomenclature it may be thought that the systematist is in a poor position to offer advice, but surely he may be permitted on the score of long and trying experience to voice some cautions.

It has been suggested that ecological terms should be chosen by priority. This idea recalls the advice which a great art critic is said to have given when asked what step should next be taken in developing one of our municipal art galleries. His unexpected counsel was to burn it up. The principle of priority might not so completely destroy the fine arts of ecology, but it would inevitably singe and blacken them. Priority is only barely tolerable in taxonomy. No systematist determines his names by it absolutely, and the most annoying disagreements have arisen from varying efforts to restrain its ill effects. Were the principle of priority of expression to be adopted in ecology, many well-selected and now current terms of relatively recent origin would have to give place to the vaguer, poorly defined terms of the earlier plant geography, or else some recent initial date would have to be fixed, and this would give great and perhaps unfair prominence to the works which happen to have been published at or shortly after that date. It has been found difficult enough for systematists to arrive at an agreement regarding this matter of an initial date, even in regard to authors of the rather remote past. It would be much harder for ecologists to make such a decision concerning a literature which is still chiefly of living authors. But, even if this matter of an original date could be harmoniously settled, the principle of priority would be a bad one. It would mean, not that the most fit, maturely considered, carefully discussed, and well defined term should be adopted, but that chance expression which happened to be used when the idea was first glimpsed. Furthermore, the matter of doubtful and partial synonymy of terms would present great difficulties in any such plan. Even aided by their far more formal descriptions and carefully preserved type-specimens, systematists often find synonymy almost impossible to unravel. Let this be a warning to ecologists.

Although this problem of terminology is so difficult that it should be taken very seriously, it need not be disheartening to the ecologist. The compilation and precise definition of a few hundred appropriate Latin terms with their vernacular equivalents in the more important European languages should not present a task of insurmountable difficulty for a well-chosen international commission, and would do wonders towards a solution of the trouble. The task is in no way comparable to that imposed by the two or three hundred thousand names with which systematic botany is weighted down.

During the brief course of its existence the progress of ecology both in the organization of earlier observations and in the discovery of a host of new facts has been flatteringly rapid. Of late, however, there has been a little cooling of enthusiasm, a barely perceptible tendency toward reaction, a slight question whether the subject of ecology will fulfill the promise of its hitherto conspicuous development. This feeling has been, if I rightly understand it, that the striking generalizations have now been made and the most accessible facts observed; that for its further progress ecology must now pass to details, and that these details will be found to have been already discovered and recorded to a considerable extent by the anatomist, physiologist, and systematist.

With this view I have no great sympathy. It is quite true that the ecologist has now reached a period of detail work in which results will come more slowly and be less spectacular, but still the point of view of ecology is admirably distinct, and the problems of the subject are endless.

In the first place, let us consider the division of vegetation into life-zones, plant formations, plant societies, etc. Who will say that this highly interesting work of the ecologist is approaching completion? His scheme as yet is but an outline map, filled out only in a few isolated areas. Great reaches of territory have been wholly unexamined. Admirable work has been done locally. Even considerable tracts, especially in Europe, have been examined in detail, and the results brought together in Engler and Drude's noble work, *Die Vegetation der Erde.* Warming, Schimper, Goebel, and others have extended ecological work to portions of the tropics of both hemispheres. In our own region there are many examples of critical work on restricted areas, as, for instance, Mr. Kearney's study of the Dismal Swamp and its environment, Professor Ganong's observations on the vegetation about the Bay of Fundy, our chairman's studies in Minnesota, Pound and Clement's organized presentation of the phytogeography of Nebraska, and Professor Cowles's interesting examination of the southern borders of Lake Michigan. Yet let any one who doubts ecological opportunity take a map of the world and note what an exceedingly small fraction of its surface has been seen by the eye of the ecologist, and what vast fields are still awaiting examination. There is not one of our states, even the smaller and more thoroughly examined Eastern ones, which does not offer to the plant geographer materials for monographic study and a volume as full of new information and valuable records as the phytogeography of Nebraska already mentioned. Just beyond the limits of our country is the great expanse of British America, readily accessible, healthful in climate, with a rich flora, taxonomically well explored and recorded by an indefatigable government naturalist, but offering for the most part virgin soil to the ecologist. Mexico, of which now even the remoter parts can be reached by rail, is a country of boundless floral wealth. With enormous mountains, wide plateaus, low tropical jungles, and extensive deserts, it offers in relatively close proximity an astonishing diversity of climate from arctic to torrid and from the parching dryness of arid sands to the most dense and oppressive moisture of the tropics. It possesses a vegetation far more varied in character and probably more rich in number of species than all the rest of the North American continent. Each mountain and valley seems to have its individual flora. To date, perhaps half a dozen trained ecologists have made hasty trips through small portions of Mexico. In their hurried records they have accomplished only the slightest beginning upon the varied and seemingly endless problems which the country offers. Although more difficult of access, Central and South America offer no less of ecological diversity and interest. Surely the unexplored territory on our own continent alone offers the ecologist the work of a century.

But it is by no means the case that these hitherto unexamined regions present to the ecologist his only opportunity. His observations can be indefinitely extended, not merely in breadth, but in depth. To the taxonomist there seems to be a serious defect in many ecological publications, a lack of accuracy arising from the author's imperfect knowledge of systematic botany. Too often the ecologist, in characterizing his plant formations and plant societies, is contented with mentioning a few of the more obvious, showy-flowered, and easily determined spermatophytes. It is rarely, indeed, that he states fully and correctly the numerous species of goldenrods, willows, rushes, sedges, and grasses, to say nothing of cryptogams, which form such a large and important part of the flora he is studying. These groups are for him inconveniently technical, and he is all too apt to sum them up in a sort of generic way by such vague expressions as "*Solidago* species," "several undetermined *Junci*," "many sedges," etc. When the taxonomist protests against this superficial treatment of important groups, the ecologist replies in a superior manner that he cares little for such nearly related species, that they intergrade, and are from his more philosophic point of view relatively insignificant; that, in fact, he believes the systematist to have split up species in these more difficult groups far beyond what is natural or practical. Several prolific ecologists have intimated that they care but little about the details of post-Grayan classification. They mention as single species such perfectly demonstrated and undeniable complexes as *Antennaria plantaginifolia*, *Viola cucullata*, *Potentilla canadensis*, and *Taraxacum officinale*.

What makes this matter the more unfortunate is that the ecologist is rarely a collector in the taxonomic sense. His lists are often made in the field, and are subject to no check or control by means of adequate and carefully preserved specimens. This course seems all the more venturesome at a time when the systematist is becoming daily more reluctant to make field determinations, being fully aware how untrustworthy and valueless such identifications are, and how impossible it is for any memory to retain the details of recent specific segregation. Under these circumstances, how can the ecologist hope to make accurate field-lists, or how, without specimens preserved as vouchers, can he expect that his catalogues will be intelligible, not to say convincing, to other botanists?

In making these strictures on certain all too common ecological methods I do so by no means in the spirit of adverse criticism, but merely with the hope of showing more clearly the great problems still ahead of the ecologist. For a writer on plant relations who contents himself with mentioning *Antennaria plantaginifolia* as though it were a single species closes his eyes to a whole vista of most interesting observations along his own line. The taxonomist has proved that, instead of being a single species, this is a highly polymorphous group of nearly related, although rarely, if ever, intergrading species. He knows that they have different ranges and habitats, and furthermore that by their parthenogenetic tendencies and the rarity of the staminate plant they offer to the biologist problems of exceptional interest. This is but one of many cases where from an indifference to the refinements of modern classification the ecologist has as yet failed to perceive lines of fascinating investigation appropriate to his own subject. Why should the ecologist by his own confession and preference be fifteen or twenty years behind the times in his taxonomic equipment?

While this is undoubtedly the rule, I am glad to say there are notable exceptions. The care with which Mr. Kearney has based his ecological study of the Dismal Swamp upon a large series of numbered specimens, critically identified and preserved at a great centre of taxonomic work, merits high praise. Other equally notable instances of conscientiousness in these matters might be cited.

In general, however, life-zones, plant formations, and plant societies have been indicated merely by the more conspicuous plants, identified largely in the field and with but little attention to herbarium records. Were ecologists from this time on for many years to explore no new territory, but merely extend their observations to the less conspicuous plants and more technical genera, were they to take full advantage of the most modern and detailed taxonomy, were they to place correctly in its ecological class each sedge and rush, each aster, lupine Antennaria, stemless violet, and Sisyrhinchium, not to speak of cryptogams, they would find no lack of profitable occupation or interesting results.

In the definition of plant associations there is almost always vagueness. To some extent this is inherent in the subject. Floras pass into each other gradually, and sharp definition is as impossible as it would be unnatural. Yet there can be no doubt that further study could make the classification more definite. At present plant formations and societies are characterized, as we have seen, usually by a few typical and conspicuous plants, other plants often being mentioned as of more general distribution, occurring promiscuously in differing ecological conditions. In examining ecological lists it is noticeable that just these less readily classified plants are in many instances those which the systematist is inclined to segregate into two or more species. It is impossible to escape the conviction that the ecologist by studying these segregations could often place their components with greater definiteness than he does at present the aggregates, thereby attaining an added completeness and precision in phytogeographic groups.

From these facts it seems clear that ecology may obtain new depth by the aid of modern taxonomy. The converse is equally true. In several matters the systematist must look to the ecologist for help in solving the most difficult problems of his field. In our present classification of plants there is still much that is artificial. On account of the overwhelming number of species to be examined and placed in the system, it has been as yet absolutely necessary to interpret each chiefly by the historic type. Every thoughtful systematist knows how arbitrary this is, and how seriously it hampers a natural characterization of individual species. The majority of plants have been first described from a very few specimens, or in many cases from a single individual, which ever thereafter remains the type of the species. That this historic type really represents the most typical form of the species can only be a matter of accident. In many cases it certainly does not. Yet, up to this time, it has often been impossible to solve by purely taxonomic investigations the difficult question which of several intergrading forms or varieties should be considered typical, central, or original, and which are secondary, peripheral, or derived.

A complicated problem is here involved. It is true that it has been somewhat obscured, although by no means hidden, by some systematists, who have thought to minimize the difficulty by the minute subdivision of their species. This, however, is obviously only a matter of words. To call a variety by a specific name does not stop its free intergradation, nor solve the problem of its origin and variability. It is certain that there are many variable species and that the variations have proceeded from a recent common type. It is further to be inferred that this typical form is in many instances still extant, but sure guides to its recognition are still a great desideratum in systematic botany. The question is one of development influenced by ecological conditions. It can be solved only by the closest scrutiny of distribution and habitat, past and present, with relation to the varying forms. Thus problems without number, of the greatest delicacy, requiring the closest observation and soundest judgment, are here opened to the ecologist who will turn his attention to questions of geographic variation in polymorphous species.

To turn now to a very different opportunity for successful work, I would call attention to the rarity of what may be called experimental ecology. It is not to be denied that some very interesting work has been or is still being carried on along this line, as, for instance, Professor Gaston Bonnier's studies of the influence of altitude upon alpine plants cultivated at different levels, but on the whole the field has been little worked. Of course, it may be said that much of what is classed as agriculture, horticulture, and forestry is a sort of experimental ecology. But in these practical branches the scientific aspect is apt to be obscured by the more conspicuous economic and æsthetic interests, and the results to ecology are not great. The field here opened is boundless.

It is one of the chief difficulties of the ecologist measuring the effects of the different forces of nature upon plant life, that they are all acting at once. Each plant when in a state of nature is simultaneously affected by the physical and chemical nature of the soil, amount of light, degree of moisture, exposure to wind, density and purity of the air, crowding of other plants, and attacks of animals. Its development is the mathematical resultant of the composition of these forces. To understand their relative influence upon the plant it is necessary to isolate them. To do this it is only needful to vary one influence while maintaining the stability of the others. Such experiments require no great ingenuity, and may even be applied to plant communities of some size; thus the addition of a single chemical substance to the soil, changing the amount or character of the light, adding or withdrawing competing plants, modifying the degree of moisture in air or soil, or controlling in some single regard the animal environment, are nearly always possible, and often very easy experiments.

It may be said that these things have all been done repeatedly by the plant physiologist. This is very true, but it is to be remembered that his point of view has been different. He has tried these experiments to learn the specific reaction upon the particular plant. To the ecologist, however, their interest would be in the comparative effect upon the different components of a flora, for it would be thus that he would gain new insight into the fundamental factors in distribution.

Professor Warming, a great leader in ecological investigation, said some years ago, "There is scarcely a more attractive biological field than to determine what the weapons are with which plants force one another from their positions." Professor Ganong, in recently commenting upon this idea, says, "To-day we know no more of that subject than when Warming wrote those words." May not this problem be simplified by reversing it? Would it not be better to begin not with the weapons, but with the vulnerability of plants? Is it not safe to assume that when certain plants give way in competition it is because they are to a greater extent subject to some one or more adverse influences? The nature of these and the degree to which each species of a community is affected by them can to a great extent be determined by experiments such as have been suggested. When the relative vulnerability of the different plants has been found, it may be logically assumed that the weapons of the more resistant are nothing other than their superior faculties of withstanding these untoward influences, forces which by artificial control may be ascertained with definiteness and measured with precision.

To this point I have spoken chiefly of the development of ecology as a pure science. Although we live in an age when the pursuit of knowledge for its own sake needs neither excuse nor apology, nevertheless, it is in its practical application that every science excites the keenest interest. An investigation void of immediate or indirect effect upon human welfare is relatively unattractive. An expert mathematician recently told me that there were great fields in his subject, hitherto unexplored, because they are too remote from any known application to physics, astronomy, mechanics, or any other branch of applied mathematics. The same is true, although perhaps to a lesser extent, in certain phases of biological work. They seem too far from probable usefulness to stimulate the investigator to their enthusiastic pursuit. This can, however, in no wise be said of ecology. Dealing as it does with the vital relations of plants to their surroundings, it yields information of the highest importance to the farmer, nurseryman, and landscape gardener. Indeed, it bridges just that all too wide gap between theoretical and applied botany, connecting the abstruse fields of plant anatomy, plant physiology, and classification with the concrete applications of botany in agriculture, horticulture, and forestry. The ecologist will never lack that wonderful stimulus which comes to the investigator who is conscious that his work is important to the welfare of his fellow beings, and intimately bound up with human progress.

SECTION F—BACTERIOLOGY

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(*Hall* 15, *September* 24, 10 *a. m.*)

CHAIRMAN: PROFESSOR HAROLD C. ERNST, Harvard University.
SPEAKERS: PROFESSOR EDWIN O. JORDAN, University of Chicago.
PROFESSOR THEOBALD SMITH, Harvard University.
SECRETARY: DR. P. H. HISS, JR., Columbia University.

RELATIONS OF BACTERIOLOGY TO OTHER SCIENCES

BY EDWIN OAKES JORDAN

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IT is possibly a contemporary delusion that we are living in a period of unexampled mental activity. The life of the intrepid modern scholar affords opportunity for self-deception. If one becomes a member of a sufficient number of learned and quasi-learned societies, and attends committee meetings for an adequate variety of purposes, the impression of profitable intellectual endeavor may be prematurely acquired. There is much, however, to account for the prevailing sensation of breathless advance. The physiologic and psychologic accompaniments of a breakneck pace are not altogether lacking in the modern world, and there are bacteriologists, in particular, who will lend a credent ear to affirmations of the rapidity of scientific progress. However this may be, few can question that the development of the science of bacteriology has been marked by an unusual tempo. To those who have followed this development closely, discovery has trod upon the heels of discovery in bewildering succession. The scant thirty years of its history have been crowded with feverish activities, which have found their best justification in the results accomplished. At present the science touches nearly many human interests, and sustains manifold and far-reaching relations to the whole body of natural knowledge. It is no matter for surprise that such should be the case with a science that owes its birth to a chemist, that concerns itself with microscopic organisms belonging both to the plant and animal kingdoms, and that extends its ramifying branches into the regions of medicine, hygiene, and the industrial arts.

In several respects the history of bacteriology might be held to epitomize that of the other natural sciences, or of the living organism itself. Advance in complexity of structure entails greater complexity of relations and adjustment; maturity has more extensive connotations than youth. Bacteriology is a relatively youthful branch of the stream of knowledge, but in late years it has perceptibly widened its banks. It has even encroached upon certain neighboring sciences. Modern physiography uses the term *piracy* to designate the capture by one stream of that portion of a watershed legitimately belonging to another stream. In the same way, one natural science, owing to peculiarities in its subject-matter, in its evolutionary history, or in the tools with which it works, may enter upon a piratic career, and appropriate territory which for various reasons has remained unexploited by the science to which topographically it may seem to belong. This annexation of neighboring fields has been not uncommon among the natural sciences, and bacteriology has not shown itself free from the general tendency. A notorious instance of piratic conduct on the part of bacteriology is the virtual appropriation of the whole field of microbiology. Perhaps most familiar in this connection are the discoveries concerning the life-histories of various microscopic animal parasites. The tracing-out of the relations between parasites and hosts in Texas fever, malaria, and dysentery has by no means been exclusively or even largely the work of zoölogists. On the contrary, it is well known that much of the most important work in this direction has been carried out by bacteriologists, and that the literature on these topics is chiefly to be found in the technical bacteriologic journals. A recent instance of this tendency is the renewed study of the remarkable protozoa called trypanosomes, which has in large part been undertaken by bacteriologists and by bacteriologic methods. Perhaps the most notable triumph yet accomplished in this field is the successful cultivation of these pathogenic protozoa outside of the animal body, a feat which has been achieved by one of the foremost American bacteriologists. The exploitation of zoölogic territory by bacteriologic workers is one of the many instances of successful borderland invasion, and, like the Louisiana Purchase, illustrates the impotence of territorial lines to prevent natural expansion. Many reciprocal piratic inroads among the sciences are due to the acquisition by one science of new tools which, when workers become generally acquainted with their use, are found to be applicable to other problems in other fields. Bacteriologic technique is one of these efficient tools the possession of which conduces to piracy; it can, however, never be forgotten that bacteriology itself owes its powerful equipment to a study of spontaneous generation which was undertaken primarily for the interest felt in its philosophic bearings.

Bacteriology stands in close relation to at least four other more or less defined fields of natural knowledge: to medicine, to hygiene, to various agricultural and industrial operations and pursuits, and to biology proper. Bacteriology, as has been often said, is the youngest of the biologic sciences, and for this reason has as yet contributed relatively little to the enrichment of the parent science. Morphologically the bacterial cell is so small and so simple as to offer many problems of surpassing interest, but of great difficulty. The question as to whether a bacterium is a cell without a nucleus, or a free nucleus without any cytoplasm, or a cell constituted in the main like those of the higher forms of life, has, to be sure, been practically settled in favor of the latter view. But there are other debated and debatable morphologic questions to which up to the present no satisfactory answer has been given, and to which our current microchemic methods are perhaps unlikely to afford any solution. On the physiologic side, the achievements of bacteriology in behalf of general biology have as yet been far from commensurate with its potentiality. This may be partly because of its temporary engrossment in other seductive lines of research, partly because of the lack of workers adequately trained in bacteriologic methods and at the same time possessed of an appreciation of purely biologic data. It may be justly urged that a rich harvest of fundamental physiologic facts waits here for the competent investigator.

There is no need to dwell in detail upon the manifold practical applications of bacteriology to the arts and industries. Particularly in agriculture and kindred occupations have the advances in bacteriology been immediately and intelligently utilized to bring forth in turn new facts and unveil new problems. The processes of cream-ripening and vinegar-making, the phenomena of nitrification, of denitrification and nitrogen fixation, the modes of causation of certain diseases of domestic plants and animals, have all been elucidated in large measure by bacteriologic workers. A new division of technologic science, dealing with the bacteriology of the soil, of the dairy, and of the barnyard, of the tan-pit and the canning-factory, has already assumed economic and scientific importance.

It is often a temptation to distinguish radically between pure science and applied science and to look upon the latter as unworthy the attention of the philosophically minded. True science can admit of no such distinction. Nothing in nature is alien to her. She can never forget that some of the most fruitful of scientific theories have been the outcome of the search for the utilitarian. Man's knowledge of the universe may be furthered in various ways. It is well known that the work of Pasteur was particularly characterized by applications to the problems of pure science of knowledge acquired in the study of the practical. One thing plays into the hands of another in wholly unexpected fashion. An attempt to improve the quality of beer gives birth to the germ theory of fermentation, and this in turn to the germ theory of disease; the chemistry of carbon compounds leads to the discovery of the anilin dyes, and these same anilin dyes have made possible the development of microchemic technique and thrown open spacious avenues for experiment and speculation; the attempt to obtain a standard for diphtheria antitoxin has resulted not only in the achievement of the immediate practical end, but in the discovery of unexpected theoretic considerations which have dominated the progress of an important branch of scientific medicine during the last five years. It will not be a hopeful sign for the advancement of science when the worker in pure science ceases to concern himself with the problems or avail himself of the facilities afforded by the more eminently utilitarian aspects of natural knowledge.

In the quarter-century of its history, bacteriology has sustained close and mutually advantageous relations with the science of medicine. This has been the scene at once of its greatest endeavors and of its greatest triumphs. To recount these would be superfluous. There is hardly an hypothesis in scientific medicine that has not been freshened and modified, hardly a procedure in practice that has not been influenced by bacteriologic conceptions. The experimental method in particular has been given new support and received brilliant justification. Experimental pathology and experimental pharmacology practically owe their existence to the methods and example of bacteriology. The security afforded by aseptic surgery has made possible physiologic exploits that could not otherwise have been dreamed of, a pregnant illustration of the way in which applied science may directly further the advance of pure science. Conspicuous as these achievements of bacteriology have been, it cannot be truly said that the field is exhausted. There is hardly an infectious disease of known or unknown origin that does not still harbor many obscurities. Some of the most difficult problems that medicine has to face are connected with the variation and adaptation of pathogenic bacteria. The phenomena of immunity, certainly among the most complicated and important that human ingenuity has ever set itself to unravel, still await their full description and interpretation. The study of the ultramicroscopic, or perhaps more correctly the filterable viruses, is being prosecuted with great energy and in a sanguine spirit. The extension of bacteriologic method into the field of protozoön pathology has been already referred to, and constitutes one of the latest and most hopeful developments in the study of the infectious diseases. Medicine, perhaps more than any other department of human knowledge, is most indebted to and maintains the most intimate relations with the science of bacteriology.

At the present time the relations of bacteriology to public hygiene and preventive medicine seem to me of particular importance, and it is upon this theme that I wish chiefly to dwell. Personal hygiene is not necessarily pertinent to this topic, but falls rather into the same province with the healing art. Matters of diet, of clothing, of exercise, of mental attitude, affect the individual, and contribute more or less largely to his welfare. But except in so far as the individual is always of moment to the community, they do not affect the larger problems of public hygiene. The pathologic changes that take place in the tissues of the diseased organism and the methods that must be employed to combat the inroads of disease in the body of the individual patient must for a long time to come remain questions of supreme importance to the human race. But over and above the treatment and cure of the diseased individual, and the investigation of the processes that interfere with the proper physiologic activities of the individual organism, rises the larger and more far-reaching question of the prevention of disease.

Racial and community hygiene are but just beginning to be recognized as fields for definite endeavor. The project may seem vast, but the end in view is undoubtedly the promised land. More and more will the problems of curing an individual patient of a specific malady become subordinated to the problem of protection. More and more will scientific medicine occupy itself with measures directed to the avoidance of disease rather than to its eradication.

Whatever else may be said of it, this is certainly the age of deliberate scrutiny of origins and destiny. Man no longer closes his eyes to the possibilities of future evolution or to those of racial amelioration. If we are to remain to a large extent under the sway of our environment, we can at least alter that environment advantageously at many points. We are no longer content to let things as we see them remain as they are. On the surface the wider relations of disease have often seemed of little significance, as, before Darwin, the so-called fortuitous variations in plants and animals were considered as simple annoyances to the classifier; the causes of this variation were deemed hardly worth investigation. The rise and fall of plagues and pestilences have been readily attributed to the caprices of the *genius epidemicus*, and it has sometimes been thought idle to ascribe recurrent waves of infection to anything but "the natural order." Another phase, entered upon later, and from which we have not yet entirely emerged, possesses its own peculiar perils. In meditating on the cosmos, the agile mind is always tempted to fill in the gaps of knowledge with closely knit reasonings or fantastic imagery. The imaginative man of science still frequently finds himself beset with the temptation to erect an unverifiable hypothesis into a dogma and defend it against all comers. It is now fortunately a truism that a more humdrum and plodding course has proved of greater efficacy in advancing natural knowledge. Theories that stimulate to renewed observation and experiment have been of the greatest service, but unverifiable speculations have often been a barrier to further advancement. Metaphysics tempered with polemic is not science, whatever be its allurements.

If the attainment of a rational position in public hygiene, community hygiene, or preventive medicine must, then, be regarded as the main objective point in the campaign against disease, it follows that the part played by bacteriology in this advance will be an important one. The relations of bacteriology to public hygiene are fundamental. The etiology of many of the most widespread and common diseases that afflict mankind is intelligible only through the medium of bacteriologic data. The modes of ingress of the invading micro-organisms, the manner of persistence of the micro-organism in nature, the original source of the infectious material, and all the varied possibilities of transmission and infection can be apprehended only through the prosecution of detailed bacteriologic studies. It is only by this means that the weak point in the chain of causation can be detected and the integrity of the vicious circle attacked. Success will inevitably depend upon a thorough understanding of the circumstances governing and accompanying the initiation and consummation of the disease process. Yellow fever cannot be suppressed by burning sulphur or by enforcing a shot-gun quarantine; the bubonic plague is not to be combated by denying its existence.

In the warfare against the infectious diseases a rational public hygiene is ready to avoid the mistake of beating the air. A preliminary survey of the possibilities reveals several distinct types of disease; those that are practically extinct or far on the road to extinction in civilized communities, those that remain stationary, or decline but slightly, and those that show a more or less consistent increase. The economy of energy would suggest that it is not a far-sighted policy for public hygiene to focus its endeavors exclusively upon those diseases that are yielding naturally before the march of civilization. The conditions under which civilized peoples live to-day are in themselves sufficient to render the foothold of many infectious diseases most precarious. What nation now fears that typhus fever will become a national scourge, or who looks to see the citizens of London driven into the fields by the Black Death? It is of course true that the continuance of this immunity can be secured only by unremitting watchfulness, although so long as existing conditions of civilized life are maintained, the recurrence of great epidemics may be relatively remote. The pestilences that once stalked boldly through the land slaying their ten thousands are now become as midnight prowlers seeking to slip in at some unguarded door within which lie the young and the ignorant. Already some once-dreaded maladies have become so rare as to rank as medical curiosities, and their ultimate annihilation seems assured.

There are other diseases, however, that civilized life, or at least modern life, appears to leave substantially unchecked, and some that it even fosters. These may be considered as shining marks for the modern hygienist. The scale between hygienic gain and loss is always in unstable equilibrium. There is no such thing as consistent improvement all along the line. As Amiel wrote in his journal, "In 1000 things we advance, in 999 we fall behind; this is progress." It is almost a biologic axiom that progress in one particular entails loss in others. To maintain the efficiency of all parts of the complex of civilization calls for eternal vigilance. It may be that while we are waxing complacent over the fact that the opportunities for infection with certain parasites are diminishing, and that other parasites are gradually losing what we vaguely denominate as their virulence, unforeseen and greater evils are raising their heads. The increasing exemption from certain diseases will itself lead to an increased prevalence of others as diversely vulnerable age groups are formed. In general, it will occur that the diseases peculiar to the advanced age groups will increase as the diseases of childhood and youth succumb to hygienic measures. A different age distribution of the population will bring in its train new problems of preventive medicine, which must be successfully solved if the issue is to be fairly met.

There are not lacking instances of a dawning consciousness on the part of mankind that the proper development of public hygiene involves a far more comprehensive view of its relations than has hitherto been taken. The study of tuberculosis is being approached by methods of unexampled broadness. We are just beginning to recognize the way in which the roots of this destructive malady are well-nigh inextricably interwoven with the whole social fabric. Bacteriologic, architectural, and economic data are all levied upon for contribution to our knowledge of what is universally recognized as one of the most important of all human diseases. Here, as elsewhere, the care and cure of the infected individual still looms large, but beyond and above this is beginning to be placed the prevention of infection, the drying-up of the stream at its source. That for this heavy task public hygiene will require the aid of many workers in many different fields is abundantly evident. For all of them, however, bacteriology must furnish the only definite point of view. In the full consideration of the "exciting causes," the tubercle bacillus can never be allowed to drop into the background. Given foul air, insufficient food, inhalation of dust, excessive and exhaustive labor, and the other deplorable accompaniments of modern industrialism, and it still must be constantly kept in mind that without the tubercle bacillus these predisposing causes would never result in a single case of tuberculosis. On the other hand, without these contributing factors the tubercle bacillus would almost sink to the level of the negligible "non-pathogenic organism." Witness the impotence of the bacillus to produce infection, or even maintain itself, in the tissues of those individuals able to live an outdoor life.

It is evident that in the case of tuberculosis the forces of civilization are on the whole working for its extinction rather than for its perpetuation. The available statistics demonstrate that before the modern movement for the suppression of the disease began, and, in fact, even before the discovery of the tubercle bacillus, pulmonary tuberculosis was already on the decline in widely separated parts of the world, — in London, in Boston, and in Chicago.[1] It is, perhaps, significant that pulmonary tuberculosis is now one of the tenement-house problems, and that as such it occupies a strictly delimited field. As yet the campaign against tuberculosis has been a desultory one, waged by a few enthusiasts without adequate material or moral support on the part of the community at large, but signs are multiplying that this condition will be a transient phase. The comparative absence of intelligent, systematic endeavor for the suppression of disease is certainly a curious phenomenon in an age of otherwise extensive coördination and organized action. The executive talents and restless energy lavished on commercial, industrial, and engineering projects may some day be turned to devising and carrying out hygienic measures. If it were necessary to find an argument in the economic value of human life, it would be readily forthcoming. The recent movements for the study and suppression of tuberculosis mark one of the first attempts to apply bacteriologic knowledge in a determined and radical way to a problem of public hygiene. As regards the ultimate extinction of tuberculosis, there may be more or less groping after ways and means, but there need be no misconception as to the scope of the problem.

There are other fields in which a similar mode of procedure based on ascertained bacteriologic facts and principles has been indicated

[1] Biggs, N. M., *The Administrative Control of Tuberculosis, Medical News*, 84, p. 337, 1904.
Vital Statistics of the City of Chicago for the years 1899–1903 *inclusive*, Chicago, 1904.

and is being at least in part carried out. In typhoid fever the evidence from epidemiology has long pointed unmistakably to drinking-water as being the chief vehicle of infection, and the first step toward suppression of this disease has been already taken in most civilized countries. The last half of the nineteenth century witnessed an improvement in the sanitary quality of public water-supplies which has diminished perceptibly the death-rate from typhoid fever .This change has been in part effected by the introduction of water from unpolluted sources, in part by the installation of sand filters. To cite a few well-known cases: For five years before the introduction of a filtered water, the annual typhoid fever death-rate in Zurich, Switzerland, averaged 76; in the five years following the change it averaged 10. In Hamburg, Germany, for a corresponding period before filtration, the typhoid death-rate was 47; after the change it fell to 7. In Lawrence, Massachusetts, under similar conditions the typhoid rate was reduced from 121 to 26, and in Albany, New York, from 104 to 38. A similar effect has been noticed where an impure water has been replaced by water from unpolluted sources. In Vienna, Austria, the abandonment of the River Danube as a source of supply in favor of a ground water diminished the typhoid fever death-rate from over 100 to about 6. In the United States the city of Lowell not long ago exchanged the polluted water of the Merrimac River for a ground water-supply, with the result that the typhoid fever death-rate was reduced from 97 to 21. In spite of these remarkable facts, there has been a lethargic slowness in profiting by the lessons that they teach. Many communities have remained to this day unobservant and negligent, and especially in the United States, the condition of the average public water-supply demands radical reform. A method that has not only reduced the deaths from typhoid fever by about 75 per cent., but has also reduced the number of cases proportionately, is worthy of universal adoption. If the fatality in all cases of typhoid fever was diminished, say from 12 per 100 cases to 3, by the use of a new drug or an antitoxin, the world would ring with the discovery. The introduction of a pure water-supply has achieved an analogous reduction in the death-rate, and confers further the enormous benefit of preventing the occurrence of a similar proportion of cases.[1] In the city of Albany, New York, the annual number of deaths from typhoid fever prior to the installation of a filter-plant averaged 89 during a ten-year period; in 1902 there were but 18 deaths from this cause, representing a diminution not only of 71 deaths, but of over 700 cases.

Important as is the function of a pure water-supply in preventing typhoid fever, it is now clear that public hygiene cannot stop here.

[1] Jordan, E. O., *The Purification of Water Supplies by Slow Sand Filtration, Journal of the American Medical Association*, 1903, p. 850.

In some countries, as in Germany, for example, where the larger cities and towns are supplied in the main with water of a highly satisfactory character, there still remains a notable residue of cases of typhoid fever. These, we know, are due to contact infection, to contamination of raw foods, such as milk, oysters, and the like, to the conveyance of the specific germ on the bodies of flies, and to similar modes of dissemination.[1] It is a fact full of significance that the existence of these various modes of spread is recognized, that they are held to be matters of public concern, and that preventive measures are being instituted under expert bacteriologic control for suppressing the existing sources of infection. One of the most difficult problems in this campaign lies in the prompt recognition and rigorous supervision of the mild and obscure cases. It may be comparatively simple to isolate and disinfect with thoroughness in the franker types of the disease, but it is not clear that the danger is most critical on this side. The application of searching and delicate bacteriologic tests is often necessary to determine the suitable mode of action. The dependence of public hygiene upon bacteriologic data and methods has rarely been better exemplified.

The vigorous warfare that is being waged against malaria in many tropical countries affords a further and striking illustration of the utilization of existing resources for the avoidance of specific infection.[2] It is hardly necessary to reiterate the obvious truth that malaria constitutes the chief and, perhaps, the only serious obstacle to the colonization of the tropics by the white races. Political and economic questions of the gravest import to mankind are bound up with the fortunes of a protozoön and a mosquito. The complex life-cycle of the malarial parasite offers an unusual number of points of attack. As is well known, several distinct views are current as to the best way of interrupting the continuity of transfer between man and the mosquito. It is conceivable that by the destruction of the malarial parasite within the body of man, the supply of parasites for the mosquito may be cut off and the circle broken at this point. If the mosquitoes are prevented from becoming infected, man is safe. It is claimed by the adherents of one school that this method has proved very effective in certain localities where it has been systematically employed. The extermination of the parasite in the blood of man by the administration of quinin certainly constitutes an important weapon in the

[1] Schuder, *Zur Aetiologie des Typhus*, *Zeit. f. Hyg.*, 38, p. 343, 1901.
Hutchinson, R. H., and Wheeler, A. W., *An Epidemic of Typhoid Fever due to Impure Ice*, *American Journal of Medical Science*, 126, p. 680, 1903.
Ficker, M., *Typhus und Fliegen*, *Archiv. f. Hyg.*, 46, p. 274, 1903.
Hamilton, A., *The Fly as a Carrier of Typhoid*, *Journal of the American Medical Association*, p. 577, 1903.
Newman, G., *Channels of Typhoid Infection in London*, *Practitioner*, 72, p. 55, 1904.

[2] *Die Bekampfung des Malaria* (Koch, R., und Ollmig), *Die Malariabekampfung in Brioni* (Frosch, P.), *in Puntacroce* (Bludau), *in der Maremma Toscana* (Gosio, B.), *etc.*, *Zeit. f. Hyg.*, 43, 1903, Heft 1.

armory of public hygiene, whether or not it prove to be the most efficient one or the most economic in execution. In this same category are to be put the attempts to prevent the infection of the mosquito by guarding malarial patients against the bite of *Anopheles*. It is obvious that this plan may often be difficult of execution, because of the impossibility of exercising efficient control over the movements of individuals suffering from latent or recurrent infection.

A second possibility consists in the general protection against mosquito bite of all persons dwelling in infected regions. The pestiferous insect may beat its wings in vain against the windows of a mosquito-proof dwelling; if it cannot come near enough to the human being to inject the contents of its poisoned salivary gland, no single case of malaria will result. In parts of Italy, it is said, this mode of prevention has been practiced with brilliant success in protecting railway employees, forced by the exigencies of their calling to reside in highly malarious localities.[1]

A third point of attack is presented in the possibility of destroying or at least arresting the propagation of the insect host of the malarial parasite. The extermination of a number of species belonging to a widely distributed and abundant insect genus may seem in itself a gigantic task to undertake. Remembering the ambiguous success that has attended the efforts of the human race to combat the ravages of certain insects injurious to agriculture, it is not easy to be sanguine concerning the speedy extinction of *Anopheles*. It is noteworthy that the most considerable triumphs attained along economic lines have been effected by the utilization of the natural enemies of the noxious forms. Efficient foes of *Anopheles* have so far not been discovered. There is no question, however, that in definite localities the numbers of individual mosquitoes belonging to malaria-bearing species may be enormously diminished by the destruction of the breeding-pools. The labors, in this direction, of English health officials in various parts of the world, have been rewarded by a decisive decrease in the prevalence of malaria.[2]

It will not escape remark that the effect of any one or of all of these protective measures is cumulative. A diminution in the number of mosquitoes, or in the number of persons harboring the malarial protozoön in their blood, or in the number of infected or non-infected individuals bitten by mosquitoes, will inevitably produce a lessening in the amount of malaria in a given region. This will in turn diminish the opportunities for mosquitoes to become infected, and will at least

[1] Celli, A., *La Malaria in Italia durante il* 1902, *Annali d' Igiene sperimentali*, 13, p. 307, 1903.
La Société pour les études de la Malaria, Archives italiennes de Biologie (1898–1903) 39, p. 427, 1903.

[2] Ross, R., *Report on Malaria at Ismailia and Suez.* Liverpool School of Tropical Medicine, Mem. 9, 1903.

put a check upon indefinite extension of the disease. It is significant that a high degree of success apparently attends the enthusiastic and persistent application of any one of the measures instanced.

While malaria, typhoid fever, and tuberculosis are to-day fairly in the field of view of public hygiene, such is not the case with a host of other maladies. A beginning is made here and there, but the vast majority of the diseases that affect mankind still lack an intelligent and organized opposition. This is partly because of insufficient knowledge. At the present time the apparent increase in pneumonia presents an imperative field for research. It seems unlikely that the available modes of attacking this disease are to be exhausted with attempts to improve individual prophylaxis. A clear understanding of the tangled web of statistical, climatic, racial, bacteriologic, and hygienic questions that environ this urgent problem of public hygiene is likely to come only through renewed investigation of the phenomena. If it is true, as some conjecture on what seems insufficient evidence, that the virulence of the pneumococcus is increasing, what is the bacteriologic strategy suited to the emergency? Or if it turn out that an increase in the number of victims to pneumonia is largely made up of those who have escaped an early death from tuberculosis, what procedure is indicated?

We cannot always take refuge from the consequences of inaction under the plea of ignorance. There are few, if any, instances in which public hygiene is utilizing to the full the knowledge that it might possess. Some responsibility rests upon those who are prosecuting bacteriologic studies to see that the bearings of their investigations are not overlooked or neglected by those who are constituted the guardians of the public health. There is here no question of the sordid self-interest or commercial exploitation sometimes miscalled "practical application." In the long run the saving of life may play into the hands of the idealist. If John Keats had not died of pulmonary tuberculosis at the age of twenty-five, the modern world would be a different place for many persons. It is not possible to estimate the loss to literature, science, and art since the dawn of intellectual life which must be laid at the door of the infectious diseases. The relations of bacteriology to public hygiene, if properly appreciated and cultivated, will lead to an improvement in the conditions of life which will enhance both the ideal and material welfare of the race, and will give greater assurance that each man shall complete his span of life and be able to do the work that is in him.

SOME PROBLEMS IN THE LIFE-HISTORY OF PATHOGENIC MICRO-ORGANISMS

BY THEOBALD SMITH

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Our knowledge of the profound influence which the microscopic organisms, known as the bacteria, exercise in the life of the globe, may be considered an acquisition of the last quarter-century. The surmises and hypotheses of the half-century preceding were then made over into well-attested facts.

The activities of micro-organisms manifest themselves in many different ways. The functions carried on by the bacteria of the soil are known to be of fundamental importance to higher plant life. The work of the bacteria producing fermentation, putrefaction, and decay is of similar importance in preparing the way for the soil bacteria and ministering to the wants of higher organisms. Out of this latter class there has arisen a group which has given these micro-organisms all the notoriety they possess. It is a small group, but formidable in that it is in partial opposition to the higher forms of vegetable and animal life. It is these parasitic forms to which I shall devote my address, as it is they which have preoccupied my attention for some years. In thus passing over large groups of bacteria I simply register my inability to properly present their claims, and I trust that others here present will fully supplement my paper by dealing with them in deserving fashion.

While bacteriology, strictly speaking, deals only with a fairly well-defined group of unicellular plant-like forms standing near the limit of microscopic vision, medical bacteriology has been gradually widening its scope to a study of all unicellular and even higher parasitic forms, which multiply more or less indefinitely and continuously for a time in the invaded body. In addition to the bacteria proper, the protozoa, and those highly important ultra-microscopic organisms which seem to have certain characters not possessed by either of the other two groups, are now frequently gathered into medical bacteriology, because of certain underlying principles of action which govern them in common as parasites.

Bacteriology differs from the older sections of biology in several important particulars. In the first place, it has been developed under the stress of practical demands. The enormous economic and sanitary significance of bacterial life has pushed forward this study very rapidly, and the problems undertaken have been suggested almost wholly by considerations arising in agriculture and medical practice.

In the second place, bacteriology, at least so far as the parasitic forms are concerned, is essentially a study of two realms, that of the parasite and that of the host, of two organizations, widely different, acting upon one another and entering into complex, reciprocal relations. The older departments of biology do not present such a complicated aspect. Thus anatomy or morphology has, at least until very recently, dealt with structure and development without considering the relation of the individual to its environment. That was relegated to physiology and pathology. With the bacteria the morphologic aspect dropped nearly out of sight because of the difficulty encountered in analyzing structures so minute and relatively simple. Even the classification gradually evolved, as more and more forms were examined, is at present very largely a physiologic one, the characters being based on the action which the bacteria exert upon the medium in which they multiply.

Then again, there was no ulterior interest in the study of bacteria as such, which is a strong impulse in many other departments of biologic science. It is what bacteria do, rather than what they are, that commanded attention, since our interest centres in the host rather than in the parasite. This tendency manifested itself in a peculiar way. As soon as bacteria could be handled in pure culture, the study prosecuted most actively was how most quickly to destroy them. Disinfection, sterilization, and all agents which act destructively upon bacteria were diligently sought for. The first impulse of the youthful branch of bacteriology was thus to destroy, rather than to study and analyze. When, some years later, the anti-bodies were discovered, the rush toward the bactericidal serums was equally manifest.

Bacteriology in its scientific form was thus ushered into existence largely by medical men who had definite practical ends in view. It presented from its beginnings a dual aspect for study, and its chief aim from the first was the destruction of one of the elements, the parasite. Slowly, however, the more impartial study of host and parasite in their mutual relation began to take root, and to-day there is scarcely a department of physical, chemic, and biologic science which does not have some share in the unfolding of this complex relation existing between plant and animal life, on the one hand, and the micro-organisms acting as parasites, on the other. As a result of this rather unique state of affairs, bacteriology is not a self-contained, well-defined field of work, but one greatly subdivided by aims and methods of study. A realm as large as that of micro-organisms may well claim attention in many workshops of science.

The short time at my disposal does not permit a wide survey of the field of bacteriology, and I have deemed it best to discuss in a general way the parasitism of bacteria and to outline the probable results of any attempts of medical and sanitary science to modify this parasitism. In undertaking this task I have adopted the somewhat discredited method of presenting actual hypotheses, partly new, partly old, in a new dress. These furnish a definite point of attack, and are better suited for discussion than any presentation which boxed the compass with the views already well known.

Infectious diseases have frequently been portrayed as a battle between two organisms, the host on the one hand, the parasite on the other. There are few diseases, even among those not strictly infectious in character, in which this battle does not go on at some stage, and in which the activity of bacteria may be ignored. For some years the analysis of this warfare has been the chief problem of bacteriology and pathology. What are the weapons of offense and defense on either side? Are the weapons simple or complex? Are they changed as the struggle progresses to suit the immediate state of the battle? Do the combatants themselves change during long or short periods of time, and does the character of the disease change as a consequence? Is the behavior of parasites, when posing for us in the culture-tube, different from that in the animal body? These and other queries may easily be read into the special literature of the last decade.

To realize the great complexity of this struggle we need but to review the gross facts of disease which express themselves in epidemics, on the one hand, in individual disease, on the other. We meet all gradations of severity, from rapid death to a mild transient disturbance, from a disease lasting hours to one lasting fifteen or twenty years, or even longer. Even the simplest generalizations concerning such a varied phenomenon must necessarily be subject to many exceptions, and perhaps gross inaccuracies. This is evident from the heated discussions which have been waged over the humoral and cellular phenomena, the antitoxic and bactericidal forces of the blood, and the phagocytic activities of certain cells, each party to the discussion claiming, at least for a time, that the opponent had no case. Though the brilliant researches of Metchnikoff and Ehrlich, and the fundamental discovery of Behring and Kitasato, have to a certain degree exposed the mechanism of warfare, the exposure is only fragmentary, and the hypothetic reconstructions based on it are leading as usual to further controversy. We do know that no two species of micro-organisms carry on the warfare just alike, and that the same parasite finds a somewhat different situation in every host attacked. The problem of the immediate future is to determine where the brilliant discoveries of Metchnikoff, Nuttall, Behring, Bordet, Ehrlich, and others belong in the life of each microbe, and to construct for each disease the exact nature of the contest.

In the following pages I do not intend to enter into any discussion concerning the intimate life of bacteria, but simply to point out certain biologic problems which seem to lie on the surface, as it were, and which illustrate the close relation existing between bacteriology and general biology. They have suggested themselves to me from the comparative standpoint, one up to the present but poorly cultivated in medical science.

The researches of Roux, Kitasato, and Behring, Van Ermengen and others, have shown that certain species of bacteria secrete toxins during their vegetative period. These toxins are soluble in the mediums in which these species multiply. Besides these physiologically well-defined poisons, there are others which are closely linked to the body substance of the bacteria, and which have become familiar to us in such well-known substances as tuberculin and mallein. According to the theory of R. Pfeiffer, this second class of poisons is liberated only by the disintegration of the bacteria, and the intoxication of the host, due to its destructive action on the bacilli, is a kind of post-mortem effect of the parasites. Other bodies, the so-called lysins, which act destructively upon red and white corpuscles, have also been demonstrated by Van de Velde and by Ehrlich and his pupils, but their significance in disease is not yet clear.

In the host, on the other hand, during the multiplication of micro-organisms, there appear bodies known as anti-bodies, which have aroused the greatest interest. They neutralize the soluble toxins, agglutinate the invading bacteria and disintegrate them. They also precipitate or coagulate albuminous bodies. Their action is specific, being directed toward the invaders. These are the main weapons which thus far have been found. Are there other offensive and defensive bodies? What course do the bacteria pursue in the presence of the gradually accumulating anti-bodies of the host? Do they forge new weapons or not?

Professor W. H. Welch in his Huxley lecture presented the theory that the mechanism of the production of anti-bodies on the part of the invaded host was set in operation by the micro-organisms as well, and that various tissue poisons might have their origin in overproduced bacterial receptors thrown off under special stimulation by host substances. This theory implies that bacteria may not unfold all their activities in the culture-tube, and that the latter give us no reliable clue as to their behavior in the living body.

On this point we may perhaps get some light by a consideration of the plasticity of micro-organisms. It has long been known that the pathogenic power of bacteria is reduced gradually in artificial cultures. It is also well known that by a series of inoculations, or passages through animals, the virulence may be restored, and even raised above the natural level. Bacteria have been gradually accustomed to originally destructive doses of poisons in culture-fluids. Very recently it has been shown that they may be gradually trained to multiply in strongly bactericidal serums and to refuse to be clumped in strongly agglutinating serums.

These adaptations persist for a certain time, and are transmitted for a limited period, even in culture. In other words, the modifications are more or less gradually acquired and gradually lost. The same is true of the anti-bodies of the host. The antitoxin circulates in the blood of the horse long after the stimulation by toxins has ceased. In the immunized animal the agglutinating properties do not disappear at once. I am, therefore, inclined to believe that the bacterium freshly removed from its usual environment will, at least for a time, exercise all its functions, provided the special nutritive substances which may be needed to carry on those functions are present.

The theory of Professor Welch would then resolve itself into a question of nutrition. In the body of the host there are certain substances which give rise to special toxins when acted upon by special bacteria. If we could offer these special substances to freshly isolated bacteria, there is no reason why the assumed toxin should not be formed. We must, therefore, take into account two possibilities, the adaptation of microbes to originally destructive agencies, and the production of poisons from specific substances elaborated by the host.

I have entered into this much of detail concerning the mutual relation of micro-organisms and host, in order to make clear the hypothesis, which, it seems to me, accounts very well for the general phenomenon of infection. It is that the tendency of all invading micro-organisms in their evolution toward a more highly parasitic state is to act solely on the defensive while securing opportunity for multiplication and escape to another host. By tendency I mean a general slow movement through long periods of time. The following data are in its favor:

(1) The production of diffusible toxins survives parasitism indefinitely, and is readily brought about in cultures.

(2) Where toxin-producing bacteria have become adapted to a definite species, as in diphtheria, the toxin itself acts upon a number of different species. In other words, the parasitic relation is far more specialized than the chief pathogenic product.

(3) No strictly invasive bacteria have yet been found producing diffusible toxins which appear to be of any real significance in the disease process.

(4) Those which produce such toxins are not strictly invasive bacteria.

(5) The injury due to invasive bacteria is known to be due to the disintegration of bacteria and the setting free of poisons locked up in the bodies of the microbes.

(6) Pathogenic bacteria manifest less biochemic activity than the related saprophytic forms.

(7) The hemolytic and leukocidic toxins of bacterial filtrates may be due to autolysis of the bacteria. Jordan has shown that hemolysis is, at least in part, due to a change in the reaction of the culture-fluid.

According to this hypothesis, micro-organisms, in slowly adapting themselves to the parasitic habit, would gradually eliminate active toxin production and other aggressive weapons as of little use, and strengthen whatever defensive mechanisms they may accidentally possess the rudiments of. If these are capable of marked development, we may expect such types of disease as tuberculosis, leprosy, glanders, and syphilis, in which the parasitic habit is carried to a high state of perfection. If their mechanisms of defense are not capable of much development, they will soon be destroyed, or else become adapted to live upon the skin, and especially the mucous membrane, as opportunists and occasional disease producers,

In this adaptation the possession of somatic poisons set free during disintegration may play an important part. They may give rise to just sufficient toxin to produce a local protecting nidus of necrotic tissue, until the time for escape to some other host arrives. This assumption is supported by the fact that diseases of some duration are usually focal in character. The micro-organisms multiply only in certain foci, which sooner or later become evident as the visible seat of disease.

It may be claimed that defensive and offensive methods are practically the same, and that it is simply a play upon words to make any distinction between them. But reflection will convince us that offensive methods mean direct injury, whereas defensive methods simply mean a neutralization of the offensive weapons or else a condition which is invulnerable to them, such as an envelope made of a special substance.

According to Ehrlich and his pupils, the anti-bodies which appear in the course of disease are not new bodies, but overproductions of bodies present in minute quantities normally. The parasitic microbe is thus at the very beginning of the invasion confronted with these bodies. At the termination of the disease there are no new bodies present, but the anti-bodies are on hand in relative abundance. The situation which the invader has to face is thus qualitatively the same at the beginning and at the end of the attack. How does he meet it by defensive methods?

Three possible fates await the invaders: (1) They are largely destroyed within the body; (2) they are excreted, or discharged through various channels; (3) they remain indefinitely in the body after the disease is over, to be eventually destroyed or eliminated.

That the micro-organisms are largely destroyed within the body in the course of the disease is not open to dispute; this class is of no special significance to us. Of most importance are those that escape to continue their life-cycle in another subject. The mechanism of elimination is of vital importance to the parasite. It assumes many forms, and is admirably adapted in the various specific diseases to perpetuate the existence of the species.

The survival of the microbes after the disease is over may be explained partly on the ground that in nearly all diseases some of the microbes pass their final stage near the surface of the skin, or mucous membrane, or in organs in direct or in indirect contact with the outer air, so that escape outward is readily effected through destruction of tissue, and hence protection from the bactericidal forces of living tissue. The small number which in some types of disease remain alive for some time after the disease process has subsided may also be inclosed in small foci of necrotic tissue, and thus escape destruction temporarily.

I am inclined to believe, however, that among the problems of the future will be the elucidation of still another mechanism for the protection and escape of the micro-organism. It is highly probable that in a certain number of species of bacteria, after the active vegetative stage a latent stage follows, during which the parasite which has escaped destruction provides itself with some protective envelope which also aids it in its passage to a new host. This envelope, which may be some specific substance not recognizable with the microscope, or which may be represented by the capsules in some groups, may be a defensive body of the parasite stimulated to overproduction by the anti-bodies of the host. This body also interferes with the metabolism of the microbe, and thus acts in the double capacity of stopping the disease and protecting the microbe at the same time. This hypothesis suggested itself to me while endeavoring to account for the peculiar behavior of tubercle bacilli under cultivation.

It is well known that tubercle bacilli from the diseased tissues of cattle grow very slowly, and then only upon certain culture-mediums, such as blood-serum. After several years of continuous cultivation they multiply vigorously in glycerin bouillon, and can hardly be distinguished in appearance from those human varieties of the bacillus which grow richly from the first or second transfer. There seemed to be no justification to assume that the bacillus had completely changed its metabolism under artificial cultivation. The more rational hypothesis seemed to be the one which assumed the existence of some protective substance only slightly acted upon by the serum, not at all in glycerin bouillon, and therefore a hindrance to multiplication. After repeated transfers, this protective substance was slowly lost, either through a selection of bacilli, or absence of stimulation on the part of the host, or both causes combined, and the growth became as luxuriant as with the more saprophytic human varieties. It is obvious that each group or species of bacteria would have its own special protective device, depending upon original capacities of the species, which would be gradually developed in power and efficiency with the perfection of parasitic relations.

The formation of protective or defensive coverings, the strengthening or modification of the cell-wall, or the secretion of defensive fluids, would account for certain phenomena which are familiar to bacteriologists much better than the current theory which bases parasitism exclusively upon toxin production, active or passive.

In cultures we should expect a loss of power to form protective substances because the anti-bodies are absent. Hence the universal tendency toward the reduction and final loss of virulence, with apparently the metabolic and vegetative activities unchanged, and the frequently observed regaining of virulence by passages through series of animals.

In the evolution of parasitic bacteria I assume, then, that though the function of toxin production may have been the entering wedge toward a parasitic existence, there is a progressive loss of this function as of little use to the parasite after it has once acquired a foothold, for the action of toxins at a distance from the focus of multiplication does not aid the parasite, while it may destroy the host. In other words, with the invasion of the tissues of the latter it became necessary for the invader to concentrate its powers in its immediate vicinity, and for this purpose those poisons set free by the disintegration of the parasite may be of use in protecting the focus where the younger forms are, by necrosis of tissue, plugging of vessels, etc., and thereby keeping away the bactericidal forces until the bacteria have accumulated sufficient protective power to subsist in a latent condition, and are ready to be discharged outward. With the loss of active toxin production according to this hypothesis, and the loss of other, now useless, metabolic activities, there goes hand in hand a strengthening of the defensive functions. This strengthening I interpret as the gradual development of certain substances which the non-immune host is unable to act upon, or at most only in a slight degree. This substance, which, as it were, shoves itself between the parasite and the common bactericidal forces of the body, bears the specific pathogenic character of the microbe. It is the substance which, according to the nomenclature of Ehrlich, calls forth the amboceptor from the resources of the host to combine with it, and thus open the way for the usual bactericidal forces or complements according to Ehrlich. The existence of this specific protective body will account for the varied resistance of animals to the same micro-organism and the relative difficulty to induce immunity. The more difficulty the body has in producing the amboceptor, the greater the difficulty in acquiring immunity.

In the departments of preventive and therapeutic medicine, the isolation of this protective substance apart from the body toxins would be of prime importance in combating disease by inducing individual resistance. In fact, the theory that the so-called immunizing and disease-producing substances are separate is not new, but has been presented under various forms. The tendency to give up the toxic extracts of bacteria, and use the latter in their entirety in immunization, pays tribute to these unknown bodies. The most prominent example of this change was the abandonment by Koch of the old tuberculin, a boiled extract, and the utilization of the entire tubercle bacilli, ground and uninjured by heat, in the production of immunity in tuberculosis.

The foregoing hypothesis, that the tendency of microbes in perfecting the parasitic habit is to act solely on the defensive, is to a certain degree supported by a phenomenon of considerable biologic importance, which I wish to discuss very briefly.

If we examine the statistics of the various infectious diseases we are struck with the relatively low mortality of most of them. There are few highly fatal plagues now known. To be sure, the mortality of many infectious diseases is regarded as formidable by sanitarians, but if we disengage ourselves from the humane view for the moment, and take the biologic standpoint, we will agree that the relatively high mortality of 25 per cent to 50 per cent indicates a very decided preponderance of the resisting powers of the human race. The odds are always against the invading microbe. This state of affairs appears for the moment to contradict the results of experimental bacteriology, which teach us that the virulence of microbes may be more or less rapidly raised by repeated passages through susceptible animals, or even through those which possess considerable resistance. The accustoming of bacteria to antiseptics, bactericidal and agglutinative serums, has already been mentioned. With this capacity for adapting themselves to the defensive mechanisms of the host, why should not the infectious diseases become more, rather than less, virulent? What is it that keeps their virulence on a low level? This problem has occupied my attention for a number of years, but only recently did a fairly satisfactory explanation present itself. Before entering upon it I have still one other phase of the problem to consider.

Of a given number of races of the same species of bacteria, the one which becomes parasitic on a given host species is not necessarily the most virulent for that species. This phenomenon impressed itself upon me during the study of a number of races of the bacillus of *Septicemia hemorrhagica*, or, more familiarly, rabbit septicemia. Races of this species have been found very widely distributed among mammals and birds. Epizoötics due to it have been described as occurring among cattle, carabao, game, swine, rabbits, guinea-pigs, fowls, geese, etc. It lives in the upper air-passages of many domestic animals in health.

The rabbit may be successfully inoculated with any of these races. Some are very virulent, for the merest scratch of the skin inoculated with them will result in death within twenty-four hours. But the rabbit is not attacked spontaneously by them, although they are ubiquitous. The race which has fastened itself upon the rabbit is one of a very low degree of virulence for that animal. Similarly the highly virulent tubercle bacillus of cattle is encountered only occasionally in man, although the opportunities for a transfer from cattle to man are very good.

On first thought, it would seem to us that the most virulent race would be the one to crowd out any less virulent races and finally to predominate. But comparative pathology shows us that the contrary may be true.

The explanation for these apparently discordant facts readily flows from a consideration of the life-history of parasitic micro-organisms. This briefly consists of three phases, the entry into the host, the temporary multiplication therein, and lastly, the escape to another host. Each step in this life-cycle must be carefully and deliberately worked out in the evolution of parasitic organisms, and each demands a special mechanism adapted to the purpose. One step is as important as the other. The parasite must find an unguarded entry, or one which yields readily to its efforts. It must have a means of defense within the body, and it must finally reach the exterior to enter a fresh subject.

As a result of these needs, each micro-organism producing disease has one or several avenues of entry and escape. In some of the protozoa there is but one avenue, and this is highly specialized and is through the body of some insect. Among the bacteria the channels of escape are less highly developed, and there may be several. As a rule, the microbe adapts itself eventually to a locus more or less in direct contact with the exterior, and in some instances the loci of entry, multiplication, and exit have coincided. If we think over the various infectious diseases of man and animals, of which we have any definite information, we shall be surprised to find in how many the points of attack are in organs or tissues in direct communication with the exterior. In the most common type of tuberculosis, pulmonary consumption, the process is almost wholly limited to the respiratory organs. In typhoid fever the process is to a large degree carried on in the intestinal wall. In dysentery and cholera it is wholly so. Even in the very protracted disease of leprosy, the skin is the chief seat of the disease, while the discharge of bacilli from the ulcers of the nose is the rule in the tuberculous type. In that exquisitely parasitic, highly specialized group of micro-organisms producing the eruptive diseases, the final process is carried on in the skin. In these diseases the mechanism of escape is the most perfect.

On the other hand, among the spore-bearing pathogenic bacteria the means of escape is uncertain. Thus the anthrax bacillus betrays its saprophytic nature, as pointed out by Koch many years ago, in its inability to produce spores within the body. Were it not for the accidental discharges of blood from the mucous surfaces and the operations of man, the bacillus might not escape at all to sporulate. Similar conditions obtain for the bacillus of tetanus and of Rauschbrand. Both produce disease probably in an accidental manner, and not as progressive parasites. Their continued existence is assured by vegetation and spore formation outside of the body, and it is highly probable that the species would continue to exist if they did not attack animal life, and that their incursions into the body are of no use to them. On the other hand, all attempts to demonstrate the production of spores in bacteria whose existence depends largely or wholly upon parasitism have thus far failed. The spore is evidently poorly fitted to parasitism, and is replaced by other devices of more adaptability.

The mechanisms of invasion and escape bear a distinct relation to the pathogenic power or virulence. It is safe to assume that those varieties or species no matter how virulent, will be eventually destroyed if these mechanisms are imperfect. In fact, the more virulent the microbe, the more rapid the death as a result of invasion, the less the opportunity for escape. Hence there will be a selection in favor of those varieties which vegetate whence they can escape. The surviving varieties would gradually lose their highly virulent invasive qualities and adapt themselves more particularly to the conditions surrounding invasion and escape. That some such process of selection has been going on in the past seems the simplest explanation of the relatively low mortality of infectious diseases. These individuals or races of microbes which invaded the host too rapidly and caused death would be destroyed in favor of those which vegetated more slowly and in tissues permitting escape of the microbe after a certain time.

We may now return to the rabbit septicemia bacillus. The reason why the most virulent type of this group does not pass to rabbits is due to the fact that there is no satisfactory mechanism of entry and escape. This presupposes a lesion, a wound as a place of entry, and the excretion and transfer into a wound in another animal. In the rabbit this difficulty is worked out in the way usual with this bacillus. The microbe adapts itself to vegetate upon the mucous membrane of the upper air-passages. Under certain conditions it invades the lungs, pleural and pericardial, more rarely the peritoneal cavity, producing pneumonia and extensive exudates on the serous membranes, and causing death. The disease of the thoracic organs evidently follows some predisposing cause, which enables the bacillus to make a temporary invasion from the mucous membrane. This incursion into the body is not essential to the life of the race. In fact, a little reflection will show that the bacteria which invaded are not likely to be transmitted, whereas those on the mucosa are readily handed down from old to young. The virulence of the bacillus is thus kept on a low level, so low that subcutaneous inoculation of pure cultures produces merely a local lesion. This type of disease is quite different from that produced by inoculation with highly virulent races. These multiply rapidly in the blood throughout the body.

We can now appreciate Pasteur's failure to exterminate the rabbits of Australia. He believed that with races of this bacillus on hand which destroy life very quickly, all that is necessary is to start the disease among rabbits, and it will tend to spread. The stricken rabbit with its blood full of germs does not offer the means for inoculating a second, and so the virulent race perishes.

We can understand, furthermore, why the bacteria associated with definite diseases in animals produce a diseased condition with difficulty after inoculation. The virulence of the specifically adapted microbe is of a relatively low order, and in the production of epizoötics various conditions must be realized which assist the micro-organism. The careful analysis of these conditions will form one of the great problems of pathology in the immediate future.

The phenomenon of the elimination of the most virulent races and the establishment of parasitic races of less invasive power I have portrayed in the simplest terms. But it is probably much more complex. The parasite, to be successful, must also stand in a definite relation to the tissue through which it enters. It is quite probable that the race of rabbit septicemia bacilli of high virulence would not be able to maintain itself in the mucus of the upper air-passages. This ability to multiply in certain places is evidently an acquisition which gives the particular race its specific character. Without doubt the bovine tubercle bacillus, though of great virulence, does not possess the specific power of entering the human body, or, it may be, of maintaining itself after entry in certain tissues, such as the lymph-nodes, except under certain accidental, favoring conditions not yet understood. Perhaps the process of cultivating vaccine virus in the skin has deprived it of the capacity for entering through the respiratory tract, and has converted it into a purely inoculable virus.

In the study of pathogenic bacteria the relative ease with which pure cultures may be obtained from the blood and other organs only accessible by way of the blood has made this a favorite way of obtaining such cultures. But it may be asked whether we are not in this way obtaining bacteria of maximum virulence. May not the non-agglutinability of some typhoid bacilli immediately after isolation be accounted for in this way? In general, the bacteria thus obtained can differ but little from the type, as they are all recently descended from a single bacillus, or a very few which caused the infection. It is different in the so-called passages through series of animals in which the usual portals of entry and exit are circumvented and the bacteria injected into the body and withdrawn therefrom directly. As a result of such passages many species of bacteria have been made more virulent, and Pasteur was able to modify greatly the unknown virus of rabies.

Besides the maintenance of virulence, and its occasional augmentation, a slow decline to complete loss of virulence may be looked for under conditions abnormal for the microbe. This probably goes on where the bacteria multiply, partly or wholly protected from bactericidal influences. The bacilli of tuberculosis, which multiply in cavities of the lungs or in muco-pus of the air-tubes in chronic cases, must be regarded as degenerating in virulence. And we actually encounter races varying considerably in pathogenic power. In the throats of well persons, or those who had diphtheria months ago, bacilli without any power of toxin production, but with all the other characters of genuine diphtheria bacilli, are occasionally encountered.

During the elimination of the more virulent races of micro-organisms, there goes on as well a gradual weeding-out of the most susceptible hosts. In a state of nature in which medical science plays no part, there must occur a slight rise in the resistance of individuals, due to selection, and perhaps acquired immunity, which meets the decline of virulence on the part of microbes until a certain norm or equilibrium between the two has been established. This equilibrium is different for every different species of micro-organism, and is disturbed by any changes affecting the condition of the host or the means of transmission of the parasite. One result of the operation of this law is the low mortality of endemic as compared with epidemic diseases. Certain animal diseases, while confined to the enzoötic territory, cause only occasional, sporadic disease, but as soon as they are carried beyond this territory, epizoötics of high mortality may result. Climate in some cases enters as an important factor, but the most important, perhaps, is the slight elevation in virulence brought about by a more highly resistant host. The most susceptible animals are weeded out, and the rest strengthened by non-fatal attacks. The virulence of the microbe rises slightly to maintain the equilibrium. In passing into a hitherto unmolested territory, the disease rises to the level of an epizoötic until an equilibrium has been established.

The same is true of human diseases, among which smallpox is a conspicuous example. The great pandemics of influenza, which seem to travel from east to west every one or two decades, soon give way to sporadic cases, and the careful work of many bacteriologists would indicate that the influenza bacilli found at present have fallen to the level of secondary invaders, and are parasites of the respiratory tract in many affections.

As pathogenic micro-organisms differ not only in the degree of parasitism attained, but also in their essential nature, a great variety of diseases is the result. In a crude way they may be arranged into three classes:

(1) Micro-organisms which live upon the skin and the mucous membranes, and invade the body only when lesions exist in these structures, or where the general resistance is impaired.

(2) Micro-organisms which appear only occasionally from some unknown but permanent focus. They produce epidemics often highly fatal, but they are successfully pushed back, because the strain cannot readily adapt itself to the new conditions.

(3) Micro-organisms which are most highly adapted for a parasitic existence, and which produce diseases of a relatively fixed type.

As regards the first class, the conditions under which they produce disease rise more and more into prominence. The factor microbe becomes almost secondary to other factors. Many of our most common diseases obey certain meteorologic laws. Thus diphtheria and pneumonia are chiefly winter diseases, because the conditions of throat and lungs which favor them are largely due to cold weather, or, we might say, the cold weather acting upon an indoor sedentary population, or one subjected to untoward influences, injures the respiratory tract. Some microbes of this class depend upon the preparation made for them by others. Thus the exanthematous diseases, such as scarlatina and smallpox, are frequently associated with or followed by the invasion of streptococci, and the majority of deaths are due to such secondary invasion. The streptococci live upon the mucous membranes, and whenever the proper opportunity comes they invade more vital territory. This group of bacteria is the frequent cause of death in chronic diseases. Some years ago Professor

Flexner pointed this out, and denominated the invasion as a terminal infection. I think that they may also be appropriately styled the parasites of the diseased state.

Among the second group we may place such diseases as Asiatic cholera and the bubonic plague. The origin of the first is unknown. The definite host of the second is probably the rat.

Among the third class we have such groups of diseases as tuberculosis, leprosy, syphilis, and glanders, on the one hand, and the eruptive diseases, on the other. The former are very chronic, protracted, the latter acute, rapid in their course. In the eruptive diseases the infection seems to depend solely upon the specific susceptibility of the individual, and immunity is easily brought about by protective inoculation.

In tuberculosis and leprosy the mode of infection is evidently very different from that of the group just mentioned. Prolonged exposure, as in family life, seems necessary to successful infection, and even then many exposed individuals escape. In tuberculosis, heredity plays a very prominent part in the eyes of the physician, because the disease appears to propagate itself in families. This is probably due to the necessity for more intimate association and repeated exposure in order that the disease might appear. Here the disease is long drawn out, the parasite may become in a sense individualized, and the attack upon a new host may have to be made repeatedly. With these highly parasitic forms the necessity for a frequent transfer to another host is slight. In leprosy, the disease may last fifteen years to twenty years, and then death ensues, usually as a result of the attack of the secondary invaders.

From the biologic standpoint which I have endeavored to present, we may conceive of all highly pathogenic bacteria as incompletely adapted parasites, or parasites which have escaped from their customary environment into another in which they are struggling to adapt themselves, and to establish some equilibrium between themselves and their host. The less complete the adaptation, the more virulent the disease produced. The final outcome is a harmless parasitism, or some well-established disease of little or no fatality, unless other parasites complicate the invasion. The logical inference to be drawn from the theory of a slowly progressive parasitism would be that in the long run mortality from infectious diseases would be greatly reduced through the operation of natural causes. But morbidity would not be diminished, possibly greatly increased, by the wider and wider diffusion of these parasites, or potential disease producers. The few still highly mortal plagues would eventually settle down to sporadic infections, or else disappear wholly because of adverse conditions to which they cannot adapt themselves.

In this mutual adaptation of micro-organism to host there is, however, nothing to hinder a rise in virulence in place of the gradual decline, if proper conditions exist. In fact, it is not very difficult to furnish adequate explanations for the recrudescence and activities of many diseases to-day, though the natural tendencies are toward a decline in virulence. In the more or less rapid changes in our environment due to industrial and social movements the natural equilibrium between host and parasite established for a given climate, locality, and race or nationality is often seriously disturbed and epidemics of hitherto sporadic diseases result. Typhoid fever will serve as one illustration of my thesis. It is ordinarily a sporadic infection, passing from the sick to the well by direct contact. Our knowledge that the infection of this and other diseases is contained in the discharges of the sick, and a growing sense of cleanliness, led years ago to the large systems of sewerage, which have made a crowded city life possible. But the removal of sewage from our immediate surroundings was the beginning of new trouble. The sewage was led into water-courses from which drinking-water came. Hence the great epidemics in place of sporadic disease. The direct transmission of the parasite on a small scale was largely checked, but the indirect transmission greatly favored. The dweller in cities with unprotected water-supply is still further endangered by the fact that the typhoid bacilli returned in the water may represent more virulent varieties than those handed down by his ancestors in rural communities. The motley population brought together by migrations from all parts of the globe bring the various races of bacilli with them to be redistributed on a large scale.

Conditions may even create diseases artificially. Thus in childbirth, the physician through want of cleanliness may in his examination actually inoculate a wounded surface with streptococci or other septic bacteria. In a hospital badly managed, such germs may be made to pass artificially through a series of individuals, and their virulence raised. In nature this could not take place, because there would be no physician. Hence the transfer would not take place. The history of maternity hospitals before the period of asepsis in surgery is a sufficient proof for the theory advanced. Hospital erysipelas and hospital gangrene were diseases artificially bred. With the introduction of the principle of asepsis in medicine and surgery, the artificially created diseases were destroyed, because the transportation facilities of the bacteria were cut off.

These illustrations indicate that so-called natural law does not stand in the way of our having highly virulent types of disease if we are ignorant enough to cultivate them. The micro-organism is sufficiently plastic to shape itself for an upward as well as a downward movement. Among the most formidable of the obstacles toward a steady decline of mortality is the continual movement of individuals and masses from one part of the world to another, whereby the partly adapted parasites become planted as it were into new soil and the original equilibrium destroyed. These various races of disease germs become widely disseminated by so-called germ-carriers, and epidemics here and there light up their unseen paths. Fortunately for us, the conditions under which these micro-organisms may establish themselves are in many cases so complex that they cannot be realized. It is highly probable that the bubonic plague cannot get a foothold or maintain itself among us, while Asiatic cholera might have a better chance, through our still greatly unsatisfactory water-supplies. Many tropical diseases would fail to take root in our climate. The mysterious rise and disappearance of leprosy in the Middle Ages has astonished many students of epidemiology. Possibly some slight bias of the micro-organism may have accomplished what seems almost a miracle. Perhaps the right race or variety, once introduced, may repeat the history of the Middle Ages in our day or in that of the coming generation.

Another obstacle to the amelioration of infectious diseases is the rapid change going on in the habits of individuals and the ferment in our conceptions of health and well-being, which are continually upsetting any established equilibrium and making us more resistant to some diseases, more susceptible to others. Of great interest is the effect upon the human race of the assiduous care of those afflicted with certain chronic diseases which is just now expressing itself in the establishment of sanatoriums for the cure of the tuberculous. If this movement should gain great headway, there may be a race of immunes gradually developed who may be able to stand the untoward conditions of indoor city life much better than the naturally robust and physically superior who have no so-called hereditary taint.

Of still greater interest is the vast vaccination experiment to whose beneficent influence the century just past bears ample testimony. The vaccinated individual is either wholly immune, or else the disease contracted after exposure is abortive, and the eruptive stage does not come to full development or maturity. The excretion of the infecting organism is thereby greatly interfered with, and it is not improbable that in the mildest cases it may not reach that maturity necessary for the successful infection of others. In view of the adaptability of micro-organisms in general, it is not beyond the range of possibility that a variety of the smallpox organism may through a chain of accidents arise as a result of successive passages through partly protected individuals. To-day it seems fairly well established that a single vaccination in infancy is not an adequate protection during life, and at least one nation — a nation which not only cultivates but consistently utilizes science — prescribes two vaccinations as necessary to complete protection. Whether in the days of Jenner repeated vaccinations were deemed necessary I have not been able to verify; but we may assume without immediate fear of experimental contradiction that a century of incomplete protection may have worked some changes in the smallpox organism. In any case, it is obvious that our thesis implies, in addition to the natural decline of virulence, also a gradual rise in virulence whenever the resistance of susceptible individuals is raised on a very large scale. Either the micro-organism, if a true parasite, will perish, or else it will augment its invasive powers to meet those of its host.

Another problem has been created for the diphtheria bacillus by the extensive use of diphtheria antitoxin. Will the thorough protection of one group of human beings lead to the decline or to the increase in virulence of the diphtheria bacillus circulating among the individuals of this group? What effect will the transfer of such bacilli to unprotected groups have? These and similar queries may be answered not many years hence, for a generation of microbes represents a very short space of time.

It may not be out of place to call attention here to the bearing of my thesis upon the recent attempts to utilize parasitism in ridding us of undesirable or noxious animals. In bacteriology there have been attempts to destroy field-mice and rats with certain species of bacteria. In entomology, parasitism is such a familiar phenomenon that it has been seized upon on a number of occasions to destroy otherwise unassailable insect pests.

Leaving out of consideration the presumptive dangers of introducing new species into a locality or country, which must always be taken into consideration, although they may be of no significance, we have to consider the chances of success as compared with the cost of introducing and maintaining the parasites. In any event, we need not expect a destruction of the noxious species, for that is not the end of parasitism. A reduction in numbers is all that need be looked for. The new parasite will probably fail to become acclimated at first, and it may be necessary to reintroduce it for a number of years. During this period some few may become adapted to their environment, and continue as parasites. Whether the equilibrium finally established will be of economic value, must be observed rather than predicted. In bacteriologic experiments of this kind the continued vigorous activity of the bacteria from year to year need hardly be expected. The disease will either die out or continue on a low level of mortality, in accordance with the general laws I have detailed, unless bacteria whose destructive powers are maintained and carefully gauged in the laboratory are distributed at definite intervals.

In conclusion, I will simply call attention to another problem affecting the future well-being of mankind, the possibility of new infectious diseases arising in the flux and change incidental to human progress. We have assumed that the capacity for a parasitic existence probably depends on some original offensive power of the microbe which it accidentally possessed, such as toxin production, or the presence of intracellular toxins combined with defensive powers. These, possessed independently of the host, were probably the entering wedges to be further developed or dropped, according to necessity. It is more than probable that all species of bacteria which possess these rudimentary invasive powers have already availed themselves of the opportunity to become parasites of animal life on the one hand, of vegetable life on the other, and that no startlingly new diseases will arise from saprophytic forms.

Subsidiary problems there are, however, concerning the modifications and readaptations of the parasitic forms already in existence. These may be grouped under two heads:

(1) The transfer and adaptation of parasites from one host species to another.

(2) The increase of invasive properties of parasites of the same host.

Are there any new diseases likely to appear as a result of the successful adaptation of parasites of higher animals to the human subject? This is a legitimate question, though difficult to discuss, for want of material at present. Among the more important possibilities I will simply mention the bovine tubercle bacillus and the hog-cholera group of bacteria. The larger number of parasites on animals are so specialized, however, their receptor apparatus, according to Ehrlich, may have been so curtailed, that parasitism on a relatively distant species may be impossible.

As regards the second problem, that microbes may gain in invasive power on the same host, the principle I have endeavored to establish would stand in the way of any rise in virulence, because the most invasive forms of a varying species would have the least chance for transmission. Whatever increase in disease-producing power may be acquired must be gained under special conditions, one of which is association with other microbes. Thus, if we could conceive of the same streptococcus, originally an inhabitant of the normal throat, as passing on account of some series of accidents through the bodies of a number of scarlatina patients, this streptococcus might thereby rise temporarily to the level of a serious menace to the throats and perhaps other organs of relatively healthy people.

Again, certain microbes, like *B. coli*, the pneumococcus and meningococcus, may, by living upon catarrhal mucous membranes, and passed from case to case, acquire enough temporary pathogenic power to cause localized epidemics under favorable conditions. Any advantage thus gained would soon be sacrificed, and the microbe return to the normal condition, unless a satisfactory mechanism of transmission could be established.

It will be seen that there are many problems before the bacteriologist, problems which have something akin to those of the student of races, varieties, and species among higher forms of life. These problems must be attacked with the same patience and pertinacity that were exercised by Mendel, Darwin, De Vries, and many others in the effort to trace the rise of new species.

In dealing with the great problems of pathogenesis and parasitism as applied to the micro-organisms in such a summary and hasty manner, and in endeavoring to trace the law of a declining virulence (and hence mortality) and an advancing parasitism, I may have left some doubts in the reader's mind concerning the ultimate value of medicine, preventive and curative, in controlling these diseases, since it might be assumed, according to the hypotheses presented, that they would take care of themselves. This impression will, I think, be dispelled by a little further development of the ideas presented.

The social and industrial development of the human race is continually leading to disturbances of equilibrium in nature, one of whose direct or indirect manifestations is augmentation of disease. In order to avoid this calamity, or reduce its force as much as possible, we must make special compensations or sacrifices to restore or maintain the normal balance. The more clearly the kind of compensatory action required is foreseen, the more promptly it is put into effect, the less disease there will be. It is the true function of medical science to discover and put into effect those compensatory movements which will counterbalance the temporary ill effects of what, for want of a more illuminating term, we call human progress.

It is largely through the phenomenon of parasitism that nature attempts to restore the equilibrium, and in this micro-organisms play the most important part. As soon as the individual falls below a certain level he may become the prey of a microscopic, or even an ultramicroscopic world. Hence the importance of bacteriology in medical science. Much has already been done in determining ways and means for the counterbalancing of the ravages of this microscopic world, but science cannot rise above natural law. It must work through it. The optimism of the world frequently places science above natural law and believes it capable of correcting any and all excesses of individuals and races. We may be certain that it will never be able to eliminate the factor of parasitism. Its most important work will continue to be to analyze this factor into its minutest details and to devise means by which this analysis may be made useful in turning aside or at least in deadening the shock of disease.

SHORT PAPER

Professor Frederick P. Gorham, of Brown University, presented a paper to this Section on "The Production of Light by Bacteria," in which were set forth both the importance of the study of photogenic bacteria and the various species which have thus far been discovered.

SECTION G — ANIMAL MORPHOLOGY

SECTION G — ANIMAL MORPHOLOGY

(*Hall* 2, *September* 21, 10 *a. m.*)

CHAIRMAN: DR. LELAND O. HOWARD, Department of Agriculture, Washington, D. C.
SPEAKERS: PROFESSOR CHARLES B. DAVENPORT, University of Chicago.
PROFESSOR ALFRED GIARD, The Sorbonne, Paris.
SECRETARY: PROFESSOR C. H. HERRICK, Dennison University.

THE Chairman of the Section of Animal Morphology, Dr. Leland O. Howard, of the United States Department of Agriculture, in calling the Section to order, briefly spoke of the enormous progress in research in animal morphology during the past decade, and congratulated the Section upon its good fortune in having as its principal speakers such representative workers in this branch of science from Europe and from America. He spoke of the wide range of the investigations which have been conducted for many years by Professor Alfred Giard, and mentioned especially the fact that among European zoölogists Professor Giard is probably the best informed concerning the investigations of American workers. His interest in American investigations, and his reviews and comments upon American publications, have endeared him to American biologists, while his own brilliant investigations have commanded our respect.

The work of Professor C. B. Davenport, the Chairman stated, was too well known to the Section to need any comment from him. His admirable work, and his acknowledged leadership of a new and important school of investigators, are generally acknowledged, and his recent appointment as Director of the Carnegie Institution Station for Experimental Evolution, at Cold Spring Harbor, is the latest recognition of this fact.

ANIMAL MORPHOLOGY IN ITS RELATION TO OTHER SCIENCES

BY CHARLES BENEDICT DAVENPORT

[**Charles Benedict Davenport,** Director of the Station for Experimental Evolution, Carnegie Institution of Washington. **b.** June 1, 1866, Stamford, Connecticut. S.B. Polytechnic Institute of Brooklyn, 1886; A.B. Harvard University, 1889; Ph.D. *ibid.* 1892. Assistant in Zoölogy, Harvard University, 1887–91; Instructor in Zoölogy, *ibid.* 1891–99; Assistant Professor of Zoölogy, University of Chicago, 1899–1901; Associate Professor of Zoölogy, *ibid.* 1901–1904; Director of the Biological Laboratory of the Brooklyn Institute of Arts and Sciences, since 1898. Member of the American Academy of Arts and Sciences; American Association for the Advancement of Science; Société Zoölogique de France; Allgemeine Entomologische Gesellschaft, etc. Author of *Experimental Morphology; Statistical Methods;* and other works and monographs on zoölogy.]

In the system of classification adopted by the organizers of this Congress the science of animal morphology is apparently to be defined so as to exclude comparative anatomy. I take it, consequently, that it is intended to include only the broader problems connected with the form of animals, — such as the phylogenetic evolution of form, the embryological development of form, and the restoration of the mutilated form, — in general, the form-producing and form-maintaining factors.

Expressed in this way the relations of animal morphology become more evident; and clearly the first and most intimate of these relations is with the morphology of plants. The separation of animal morphology from plant morphology in the department of biology, while according with a division of the subject found to-day in our universities, is, I think, not an ideal condition. For the form-producing and the form-maintaining factors are, at bottom, the same in all organisms. The problem of what factors have worked to determine whether a fish or a man shall have such and such a form is identical with that of the determination of the form of a fern or an oak. Little by little the morphologists that deal with the broader aspects of their science are being forced to face the absurdity of its division on the basis of the material studied. In cytology it is found that the maturation of the germ-cells, the fertilization of the egg- and cell-divisions, are identical processes in the two "kingdoms."[1] To admit a plant cytology and an animal cytology is only less absurd than to admit a mammalian cytology, an avian cytology, and a reptilian cytology.

What is true of cytology is true of the other branches of morpho-

[1] The most recent and best general work on cytology is that of E. B. Wilson, *The Cell in Development and Inheritance*, 2d edition, New York, 1901.

logy, such as embryology in its broadest sense, the phenomena of regeneration and regulation in organisms,[1] and especially the evolutionary history of specific forms. While in taxonomy we must continue to have botanists and zoölogists, as we shall continue to have ornithologists, entomologists, etc., yet outside of the purely descriptive subsciences I would the gulf between botanists and zoölogists were annihilated, and that we had biologists separated rather in regard to *subjects*, and university chairs, journals and societies devoted to evolution, cytology, ontogenetic processes, and form regulation, without regard to the systematic position of the material studied. Then we might hope to advance a subject instead of mulling over endless descriptive details.

We have next to consider the relations of morphology to form evolution, or phylogeny. Before we can consider how a new form arises, we must clear the field by seeking some element of form. The mass of material in the organic, like that in the inorganic world, early led to an attempt at the classification of these materials in both biology and chemistry. In chemistry a certain number of kinds of materials have in course of time been catalogued and are called substances, each of which has its particular *molecular* composition. In biology, likewise, many thousand kinds of organisms have been catalogued, and these are called species, each made up of particular sorts of *individuals*. Chemistry has gone a step farther in its analysis of non-living matter, and recognized that the different molecules are made up of diverse combinations of a relatively small number of units called atoms. To-day biology has to recognize that its individuals are likewise diverse combinations of units — relatively very numerous — which, following De Vries,[2] we call unit characters, or we may use the simpler name of "characteristics." Characteristics are thus to individuals what atoms are to molecules. As the qualities and behavior of molecules are determined by their constituent atoms, so the essence of the individuals of any species is determined by its constituent characteristics. And as we may construct new substances at will by making new combinations of atoms, so we may produce new species at will by making new combinations of characteristics. The making of new combinations in molecules or species is a useful work, but it is not evolution. Evolution in the non-organic or the organic world is first achieved when we can make new atoms or new characteristics, as the case may be.

This conception of species, which has arisen during the present

[1] See T. H. Morgan, *Regeneration*, New York, 1901.

[2] Compare De Vries: *Die Mutationstheorie*, "Die *Eigenschaften* der Organismen aus scharf von einander unterschiedenen *Einheiten* aufgebaut sind." Bd. I, p. 3, Leipzig, 1901.

decade, has its germ in the work of Mendel,[1] and, in consequence of the stimulating researches of De Vries,[2] Correns,[3] Tschermak,[4] Bateson,[5] and others,[6] has developed into a stately doctrine, a doctrine which bids fair to revolutionize biology as the atomic theory did chemistry. It adds at once a new dignity and interest to morphology as well as to the description of species, or taxonomy. In describing the form of an animal we are enumerating its qualities. Many of these are directly the unit characters of the species; others are composite and may be analyzed, by appropriate methods of breeding, into the elemental characteristics.

I may illustrate this by reference to domesticated poultry,[7] to which I am now paying some attention. It is impossible to enumerate all of the characteristics of poultry, but the following are some of the most striking:

Size: Large and dwarf, which are exemplified in the Asiatic breeds and the bantams.

Colors: Black; buff or red; white; brown (in the female), the male being often bronze, green, black, yellow and white; barred

[1] Mendel's work was first published in *Verhandl. naturf. Verein in Brünn, Abhandlungen*, IV, 1865. Published 1866. A translation in English is given by W. Bateson, *Mendel's Principles of Heredity*, Cambridge [England], 1902.

[2] De Vries (*Sur la loi de disjonction des hybrides, Comptes rend. d'Académie des Sciences*, Paris, CXXX, 845–847, 1900), and C. Correns (*G. Mendel's Regel über das Verhalten der Nachkommenschaft der Rassenbastarde, Ber. Deut. Bot. Ges.* XVIII, 158–168, 1900) rediscovered Mendel's paper simultaneously.

H. de Vries, *Ueber erbungleiche Kreuzungen, Ber. Deut. Bot. Ges.* XVIII, 435–443 (1900); *Sur les unités des characteres spécifiques et leur application à l'étude des hybrides, Rev. gén. de Botanique*, XII, 257 (1900); *Die Mutationstheorie*, Bd. II (1903).

[3] C. G. Correns, *Ueber Levkoyen-Bastarde, Zur Kenntniss der Grenzen der Mendel'schen Regeln, Botan. Centralbl.* LXXXIV, p. 97 (1900); *Ueber Bastarde zwischen Rassen von Zea Mays, Ber. Deut. Bot. Ges.* XIX, 211 (1901); *Bastarde zwischen Maisrassen, Bibliotheca Botanica*, Heft 53 (1901); *Ueber Bastardirungs-Versuche mit Mirabilis-Sippen, Ber. Deut. Bot. Ges.* XX, 594–608 (1903).

[4] T. E. Tschermak, *Ueber künstliche Kreuzung bei Pisum sativum, Zeitschr. f. d. Landwirthsch. Versuchswesen*, III, 465–555 (1900); *Weitere Beiträge über Verschiedenswerthigkeit der Merkmale bei Kreuzung von Erbsen und Bohnen, ibid.* IV, 641 ff. (1901); *Ueber Züchtung neuer Getreiderassen mittelst künstlicher Kreuzung, ibid.* IV, 1029. *Die Theorie der Kryptomerie und des Kryptohybridismus, Beihefte z. Bot. Centralbl.* XVI, 25 pp. (1903); *Weitere Kreuzungsstudien an Erbsen, Zeitschrift f. d. Landwirth-Versuchswesen in Oesterr.* 106 pp. (1904).

[5] W. Bateson and E. R. Saunders, *Experimental Studies in the Physiology of Heredity, Reports* to Evolution Committee of the Royal Society of London, I, 160 pp. (1902).

[6] A few important papers may be cited: W. E. Castle and G. M. Allen, *The Heredity of Albinism, Proceedings* of the American Academy of Arts and Sciences, XXXVIII, 601–622 (1903); W. E. Castle, *Heredity of Coat Characters in Guinea Pigs and Rabbits. Papers* of the Station for Experimental Evolution, no. 1 (Carnegie Institution of Washington, 1905); C. C. Hurst, *Experiments in the Heredity of Peas, Journal* of the Royal Horticultural Society of London, XXVIII, 483–494 (1904); L. Cuénot, *L'Hérédité de la pigmentation chez les souris, Arch. de Zool. expér.* X, notes, 27–30 (1902), *ibid.* I, notes, 33–41 (1903); *ibid.* II, notes, 45–56 (1904).

[7] Extensive books have been written on the different races of poultry. The following are the most important of those in English: W. B. Tegetmeier, *The Poultry Book*, London, Routledge, 1867; L. Wright, *The New Book of Poultry*, London, Cassell & Co., 1902; *The Poultry Book*, New York, Doubleday, Page & Co.

(as in the Plymouth Rock) and spangled (having centre of feather of different color from periphery).

Comb: Single, pea, rose (flat, covered with tubercles, like a file), walnut; replaced by crest.

Legs: Feathered, featherless; black, blue, yellow, horn-color.

Body-shape: Short and chunky; tall and slender.

Now the various varieties of fowl are made up of various combinations of these characters. Thus we may have Plymouth Rocks which, instead of having bars, are pure white, or all buff; or the single comb may be replaced by a rose comb (when they are called Wyandottes); the usually clear legs may be feathered; and, finally, they may be "bantamized."

Any desired characteristic in the whole catalogue of poultry characteristics might be engrafted upon an original Plymouth Rock stock. We might put on it the crest of the Polish fowl or the twisted feathers of the frizzle, or the loose barbs of the silky, or the taillessness of the rumpless, or the long tail-feathers of the Japanese long-tailed fowl. All this is, of course, possible because of the cross-fertility of the races having these different characteristics. By similar procedure we might make a white, blue-eyed, deaf, long-haired, tailless, seven-toed cat; engraft the horns of the Dorset sheep upon the hornless Southdown; add the fecundity of the two-nippled horned Dorset to the multi-nippled condition of Dr. Alexander Graham Bell's flock.[1] We might expect, after some experience, to do this with the same certainty that we can get calcium chloride and carbonic acid out of a mixture of hydrochloric acid and marble.

The bearing of this illustration, I repeat, is to show us that characteristics of species are entities, not a little of whose interest lies in the question of their origin in each case. When we know how such characteristics arise, then we may call them forth at will, and so determine the evolution of organic form. For the present it is sufficient that by the acquisition of new characteristics new species have arisen from preceding ones.

This assertion is justified by the examination of any extensive synopsis of species. Take, for example, De Bormans's synopsis of Forficulidæ in *Das Tierreich*.[2] Take any synoptic key at random. *Apterygida japonica* has two large tubercles at the end of the abdomen. *Apterygida allipes* has four small ones. *Anisolabis xenia* differs from *A. littorea* by slightly smaller size, and especially by having two teeth in the forceps in the male, or three in the female, instead of none at all. I do not mean to assert that species have arisen *only*

[1] Bell has given an account of his flock in *Science*, IX, 637, May 5, 1899, and *Science*, XIX, 767–768, May 13, 1904. He has also published privately (1904) a catalogue of his sheep.

[2] De Bormans, A., and H. Krauss, 1900, *Das Tierreich*, 11 *Lief. Forficulidæ and Hemimeridæ*, Berlin, xvi + 142 pp.

by an addition or subtraction of characteristics, but this is a common method. Very often we find one characteristic being replaced by another. Thus in Lepidoptera one species may differ from another in the replacement of red by yellow; or one earthworm will differ from another by having the sexual openings in different segments. We have no reason for thinking that these characteristics are not integral entities as much as those distinguishing domestic races. The modern morphologist, therefore, with the significance of characteristics in mind, must appreciate that in enumerating these characteristics he is enumerating the steps of evolution.

The relations of morphology to embryology are so intimate that the latter is commonly reckoned a subdivision of the former. Certainly the interpretation of the adult form depends on a knowledge of its development. "In terms of the ancient riddle," says Bateson (*Nature*, vol. LXX, p. 412), in his recent address as president of the section of zoölogy in the British Association, "in terms of the ancient riddle, we must reply that the owl's egg existed before the owl, and if we hesitate about the owl we may be sure about the bantam." The characteristics of the adult form are implicit in the fertilized egg, and are determined by the *Anlagen* of the characteristics wrapped up in that egg. We know now that upon the symmetry of the egg and of the successive cleavages often, if not typically, the symmetry of the adult form depends,[1] and that to the lack of symmetry of cleavage in gasteropods their lack of symmetry is probably to be referred.[2] In the successive cleavages definite organ-tracts are marked off,[3] and still later the epidermal organs, such as hair, feathers, and scales, — the bearers of the more evident heredity characteristics, — are laid down in regular lines, radiating often from single points or groups of cells,[4] thus simplifying the problem of

[1] H. E. Crampton, 1894, *Reversal of Cleavage in a Sinistral Gasteropod*, *Annals of New York Academy of Science*, VIII, 167–170.

[2] E. G. Conklin, *The Embryology of Crepidula*, *Journal of Morphology*, XIII, 1–210, April, 1897.

[3] Compare the results of H. E. Crampton, *Experimental Studies in Gasteropod Development*, *Archiv für Entwickelungsmechanik*, III, 1–19 (1896), in which the removal of an early cleavage cell led to a corresponding defect in the larva. Even more striking are the results of E. G. Conklin with ascidians, *Organ-Forming Substances on the Eggs of Ascidians*, *Biological Bulletin*, VIII, 205–230, March, 1905, who finds organ-tracts preformed in the uncleft egg.

[4] That metamerically repeated organs are laid down from definite bands of cells, sometimes originating in "pole-cells," has long been known, through the studies of Hatschek and of Whitman, *Contribution to the History of the Germ-Layers in Clepsine*, *Journal of Morphology*, I, 108–179 (1887). Compare also the following: E. B. Wilson, *The Embryology of the Earthworm Journal of Morphology*, III, 388–450 (1899); E. B. Wilson, *The Origin of the Mesoblast-Bands in Annelida*, *Journal of Morphology*, IV, 205–219; W. M. Wheeler, *Neuroblasts in the Arthopod Embryo*, *Journal of Morphology*, IV, 337–344. That multiple organs of other sorts are laid down in lines appears for feathers from the work of Nitzsch, *Pterylography* (1867), translated by P. L. Slater, Ray Society; and for hairs, J. C. H. de Meijere, *Ueber die Haare der Säugethiere, inbesonders über ihre Anordnung*, *Morphologische Jahrbuch*, XXI, 312–424.

inheritance of peculiarities of plumage or coat color by referring them back to transmission through particular cells or cell-groups. It has thus been possible to show that all the numerous dorsal appendages of the nudibranch mollusk *Eolis* are derived from material split off in a regular manner and at regular intervals from a group of cells lying in the tail-end of the developing animal.[1] Thus the interpretation of the mechanism of transmission of qualities is first gained from a study of embryology.

A second way in which embryology has been regarded as indispensable to morphology is in the light it has thrown on homology. By homology — the will-o'-the-wisp of morphology — is meant such a similarity of unlike things in different species as would justify their receiving the same name. And one of the strongest grounds of a homology is similarity of origin regardless of function or even ultimate anatomical connections. The search for homologies has led to the idealization of the "type," and this, more than anything else, has blinded morphologists to the facts of variation and evolution. When, however, twenty-two vertebræ in place of twenty-one can nonplus the seeker after homology, its ethereal nature is sufficiently indicated.[2] Homology may, indeed, exist between normal types, but the abnormal or pathological is often beyond homology, and yet just the abnormal is, paradoxical as it may sound, the important for evolution.

As we study an organism's form, we see that it is not made up merely of a great number of characteristics, but that these characteristics are, on the whole, such as enable the animal to thrive in its environment. We are struck by their "adaptive" nature.

I am well aware that twenty years or so ago this side of morphology — the side, namely, of the accounting for an organism's form on the ground of use — was little cultivated. Morphology had for its aim the discovery of the interrelation of parts in the individual organism and the homology of parts in different individuals or species, and if it sought to go farther it indulged only in speculative inferences as to the probable function of the parts. On the whole, the student's attention was directed towards connections of organs and his natural inquiry as to use was stifled. Some one said that function varies while the form persists.[3] This phrase became a dogma, and function was considered a matter too trivial for consideration. Homology was the study for men of science; analogy was for the dilettanti. Morphologists should have been warned by cases like the whale, whose teeth cannot be homologized with those

[1] C. B. Davenport, *Studies in Morphogenesis*, I, *On the Development of the Cerata in œolis, Bulletin of the Museum of Comparative Zoölogy*, Harvard College, XXIV, 141–148, 1893.

[2] See W. Bateson, *Materials for the Study of Variation*, 28–33 (1894).

[3] Sometimes called "Dohrn's Law."

of other mammals, and not have underrated the limitations of homology nor the importance of the study of adaptations. Only within the last few years have we come to recognize that every organ is more than a homologue: it is also a successful experiment with the environment.

The existence of that relation between form and environment which we call adaptation has been recognized for centuries, yet its full significance is still obscure. The prevailing theory (of Darwin) assumes that a change in environment precedes any change in form and that adaptation is, therefore, necessarily achieved by a change in the mean of the form to meet the changed demands of the new environment. This theory may, indeed, be said to be the natural outcome of the morphological doctrine of fundamental fixity of type. The type could be bent to meet new conditions, but could receive nothing new nor suffer loss of parts. I find that in the pre-Darwinian epoch Prichard [1] suggested that the Creator made the various species and placed them in habitats for which their structure fitted them. We see in this suggestion translated into modern terms the germ of a very different theory of adaptation from the prevailing one. I expressed this nearly two years ago about as follows: [2] "The world contains numberless kinds of habitats or environmental complexes capable of supporting organisms. The number of kinds of organisms is very great; each lives in a habitat consonant with its structure." Each species is being widely dispersed, while, at the same time, it is varying or mutating. By chance, some variants of the species get into an environment worse fitted for them; others into one better fitted. "Those that get into the worse environment cannot compete with the species already present; those that get into a habitat that completely accords with their organization will probably thrive, and may make room for themselves, even as the English sparrow has made room for itself in this country. This process may go on until the species is found only in the environment or environments suited to its organization. As Darwinism is called the survival of the fittest organisms, so this may be called the theory of segregation in the fittest environment."

The principle that animals are found in habitats for which their

[1] J. C. Prichard, *Physical History of Mankind*, 3d ed., 1836–37, vol. I, p. 96: "The various tribes of organized beings were originally placed by the Creator in certain regions, for which they are by their nature peculiarly adapted." I owe this reference to F. Darwin's *More Letters of Charles Darwin*, vol. I, p. 45, New York, Appleton.

[2] *The Animal Ecology of the Cold Spring Sand Spit, with remarks on the Theory of Adaptation, The Decennial Publications* of the University of Chicago. Preprint dated Jan. 1, 1903. This was written in the autumn of 1902. The sentences quoted are on page 21. The same idea is worked out in my paper, *The Collembola of Cold Spring Beach, with special reference to the movements of the Poduridæ, Cold Spring Harbor Monographs*, II, pp. 24, 25, July, 1903. In T. H. Morgan's book, *Evolution and Adaptation*, this view is adopted. This book was published in November, 1903.

structure fits them, and not elsewhere, points to the close relations existing between morphology and geography. We find the animals of the seashore, such as sponges, hydro- and anthozoa, and tunicates, to be largely sessile, and, in consequence, of the radiate type of structure. This sessile habit makes it possible for them to maintain their hold on the rocks from which the beating waves tend to tear them. Those which are not actually permanently attached have means enabling them to cling closely to the rocks; such are the echinoderms, the mollusks, many annelids and crustaceans. The animals of the surface of the sea, such as siphonophores, ctenophores, jelly-fishes and larvæ, are without such clinging organs; they include species whose organization permits them only to float or swim at or near the surface. The deep sea could have been populated more readily, so far as proximity goes, from the surface organisms than from those of the shore-line; but only the latter offered the structural features consonant with life at the sea-bottom, and so the deep sea became populated thence. In the swift-flowing rivers we find powerful swimmers or animals that can hold fast to the bed of the stream and in ponds, we find those species which have some means of preserving their continuity in time of drought. In caves [1] we get not any forms which happen to be washed into them, but only darkness-, moisture-, and contact-lovers. In deserts whole groups of animals are absent, only those occurring with thickest skin, — least apt to lose water by transpiration, — such as certain snakes, lizards, and hard-shelled beetles.[2] In general, in studying the geographical distribution of animals in environments presenting extreme conditions we find that they clearly have been selected from groups presenting the most favorable characteristics. All of this indicates that, often at least, the already existing morphological conditions have determined the fitness of a species to cope with the environment — morphological characteristics have determined geographical and climatic distributions.

Morphology as the science of form is often contrasted with physiology, the science of function. Yet between the two is the closest possible relation, because an organ implies a function, and every morphological characteristic has a corresponding physiological characteristic. As physiological characteristics are transmissible in the same way as morphological, we may think of any individual as being made up of such functional characteristics, just as a molecule is made

[1] Compare C. H. Eigenmann, *Cave Animals: Their Character, Origin, and their Evidence for or against the Transmission of Acquired Characters*, *Proceedings* of American Association for the Advancement of Science, Forty-eighth Meeting (1899), p. 255. Also P. C. K. Absolan, *Einige Bemerkungen über mährische Hohlenfauna*, *Zoologische Anzeiger*, XXIII, 1–6 (1900). For a popular account of our caves and their fauna, see W. S. Blatchley, *Gleanings from Nature*, pp. 99–178 (1899).

[2] For a delightful and accurate general account of the animals of our native deserts, see John C. Van Dyke, *The Desert*, New York, 1901.

up of atoms, and in the transfer from one race or species of a set of morphological characteristics, we transfer likewise the corresponding set of physiological characteristics. Thus, to return to poultry, we find the rate of growth, the age at maturity, the egg-production, the brooding instinct, and the resistance to disease, to be characteristics of various races, and it is quite possible to combine such characteristics — in so far as they are not incompatible — in various ways. Thus we have poultry that mature early, lay many eggs, and are not broody — of these the white Leghorn is a good example. Or, we may have poultry that grow large, mature late, lay throughout the winter, and are very broody — such are the Cochins. This similarity in capacity for making combinations which we see between physiological and morphological characteristics proves their close kinship and the unscientific nature of the division which would relegate their study to distinct sciences.

What is true of domesticated races is true also of wild species. Biology has suffered from the circumstance that species have been studied almost exclusively from dead specimens. Attention is focused on proportions in the dimensions of bones, on number of spines, on antennal joints, on shell-markings, and so on, and we seem to have overlooked entirely the fact that all these characters constitute only one face of the shield. The structural descriptions of the systematist give us a no more adequate idea of the characteristics of species than does the sight of this exposition on a Sunday, when all wheels are stopped and only the form, beautiful and grand as it is, remains, give us an adequate idea of it. And so in the study of species we cannot understand the form characteristics without considering also the function characteristics. I may illustrate this by some studies which Miss Smallwood[1] has been making at Cold Spring Harbor. She started with a species of Amphipoda — *Talorchestia longicornis* — that lives on the beach where it is rarely covered by the tide. After studying its form and behavior for several months she investigated a second species of the same family of *Orchestidæ*, *Orchestia palustris*, that lives on the salt marsh to the limit of the highest tides. After studying this for some weeks with respect to behavior correlated with structure, she has begun on still a third species of the same family, *Alorchestes*, which is a typical aquatic organism. The instructive thing that comes out of her studies is that in just the same way as these species differ in structural characteristics they differ in functional characteristics, and the two kinds of differences go hand in hand, and they have to be studied together to be fully intelligible.

In still another way are the dynamical and static characteristics

[1] Mabel E. Smallwood, *The Beach Flea, Talorchestia longicornis*, *Cold Spring Harbor Monographs*, 1, May, 1903. Compare also her paper, *The Salt Marsh Amphipod, Orchestia palustris*, *Cold Spring Harbor Monographs*, 3, March, 1905.

bound together, for every form or part has not merely a form or function, but a development, and development is a dynamical process. A decade or two ago embryological development was regarded as a purely morphological subject, as a series of stages, and little attention was paid to the causes that produce the stages and the succession of organs. During the last decade, however, partly under the stimulus of physiologists who have entered the field of embryology, its dynamical problems have been studied also by morphologists. As a result of the researches of Loeb, Driesch, Herbst, E. B. Wilson, Morgan, and many others, we have come to recognize that the egg is organized, — cytoplasm as well as nucleus, — and that it exhibits varying degrees of organization in different cases. Sometimes it seems as though every part of the egg was totipotent, as in the medusæ; in other cases, the different parts of the cytoplasm seem told off to develop into particular and definite organs, as in some mollusks. We have learned, further, that at every stage new organs are called forth and their development directed by stimuli proceeding from already existing organs.[1]

Moreover, it has been found that even adult structures are dependent upon external conditions for their form. It appears that peculiar functioning may alter the form of internal organs, as has been demonstrated in the case of a ship's trimmer and of a cobbler by Lane,[2] and as a vast number of pathological cases testify, such as the alteration of the arrangement of plates in the spongy tissue in the head of the femur,[3] and the functional hypertrophy of the other kidney after the loss of one. Morphologists have been forced to realize that form and structure cannot be dealt with aside from function and behavior. Every part of the living body is a sensitive, responding part whose sensitiveness determines structure. This is seen particularly well when the body is mutilated or a part removed; then begins the wonderful process of regeneration or regulation by which, under control (in the higher animals) of the nervous system, the lost parts are in many cases restored. In truth, the work of the morphologist has extended into the realm of the form-developing and form-maintaining factors, and this is a physiological realm.

From these experiences I conclude that the morphologist who studies form characteristics only is too narrow. *Characteristics* in their two-

[1] The literature on this subject is extensive; recent résumés are given in E. B. Wilson's *The Cell in Development and Inheritance*, 2d ed., 1903; also, T. H. Morgan's *Regeneration*, New York, 1902. Read also E. B. Wilson, *The Problem of Development, Science*, XXI, 281–294, Feb. 24, 1905.

[2] Lane's papers were published in the English *Journal of Anatomy and Physiology*, fifteen or twenty years ago.

[3] On the architecture of the spongy tissue of the head of the femur, see H. Meyer, *Archiv für Anatomie u. Physiologie*, 1869; J. Wolff, *Virchow's Archiv für pathol. Anat.* L (1870) and LXI (1874); also Roux, *Gesammelte Abhandlungen*, and Roux, *Der Kampf der Theile im Organismus*, Leipzig, p. 27, 1881.

fold aspect of form and function should be the object of his investigations — their difference in allied species, their integrity, their behavior in breeding, their phylogenetic origin, their embryological development, and their maintenance in the adult.

Morphology has relations with sciences quite outside of biology. I have already insisted that the problems of form and structure are also physiological problems, but in last analysis they are, I think, problems of physics and chemistry. For myself, I have no doubt that we shall some day be able to prove that each characteristic of an organism depends upon a specific substance in the germ-cell, and we may hope by altering this substance experimentally to change the corresponding characteristic. Such a change is mutation, and mutation in last analysis, as De Vries maintains, depends upon external conditions.

Apart from this it is certain that the physiological processes involved in the individual's characteristics are modifiable, and, indeed, controlled by physical agents in the environment.[1] Thus it has been possible to show that certain salts play special rôles in the development of particular organs or characteristics (Herbst). Loeb, indeed, has shown that regeneration of hydroids does not occur in the absence of potassium. We know, likewise, that iron is necessary to the formation of the chromatin of the nucleus.

The physical conditions have likewise an influence in morphogenesis. The rate of development is controlled within limits by temperature; the number and position of stomata and of leaves by light and moisture; the number and form of plant hairs by moisture; the position of branches and leaves on a stem by gravity; the formation of a hydranth in a hydroid stock by light. So evident is this dependence of morphogenesis upon physical agents that two individuals of the same family develop alike only under the same conditions of environment.

There remain to be considered the relations of morphology to the queen of the sciences, — to mathematics. Until recent years little relation has been recognized, and this I attribute to the fact that few naturalists have a type of mind that attracts them to mathematics. They have usually been led to their science through a love of nature, — a passion that belongs rather to the poetic type of mind than to the severely precise mathematical. And so I find that, even to-day, when the bearing of mathematics on morphological problems cannot be overlooked, few morphologists take an interest in the subject of biometry by which the two sciences are connected.[2]

[1] References to the literature on this general subject up to five or seven years ago will be found in my *Experimental Morphology*, New York, vol. I, 1897; vol. II, 1899.

[2] For references on biometric subjects I may be permitted to refer to my *Statistical Methods*, 2d ed., New York, 1904, which includes also a summary of results.

The fact that few morphologists have a taste for mathematics cannot stay the inevitable trend of the science toward greater precision of expression and toward mathematical analysis. Until recent years characteristics have been described only in the crude language of adjectives and adverbs — where greater precision is necessary, quantitative expression is inevitable. So we have seen during the past ten years the rise of biometry and its application to many morphological problems. Biometry had its beginning in the suggestive investigation of Galton; its great development in the last ten years has been due, above all, to the tremendous activity of Karl Pearson and the workers he has gathered about him. By the aid of efficient methods of analysis we are able to state quantitatively not only the mean value of any measurable characteristic, but also the degree of its variability and the closeness of associated variability of two interdependent organs. Moreover, it is possible to study the nature of the variability exhibited by any characteristic in any homogeneous lot of individuals and to draw an inference from the nature of this variability — as exhibited in the variation polygon — concerning the condition of the characteristic in question in the given race. A person of experience can tell from a glance at the variation polygon whether the race is in a condition of equilibrium so far as this characteristic goes, or whether it is breaking up into several forms, or is, perhaps, evolving into some other condition. The quantitative expression gives a means of measuring change of the mode from epoch to epoch which Weldon used in studying the crabs at Plymouth, and which enabled him to demonstrate a progressive change in form. It gives also a means of measuring the alteration of an organ in different environments, and so of estimating the effects of changed external conditions. Thus it has been shown that the modal number of ray flowers in the ox-eye daisy depends upon the conditions of nutrition in the soil; the chela of the male crab, *Eupagurus*, is relatively smaller in *deep* water; the mud-snails, *Nassa*, of *brackish* water are depauperate.

Again, mathematical methods have given us a measure of the correlation between organs, so that, the exact relation between human stature and the length of a long bone being known, the stature of extinct races may be calculated from a collection of disinterred femurs. Pearson has been able to show that there is no correlation between shape or size of the head and intelligence, and to demonstrate the efficiency of vaccination and the non-inheritableness of cancer. The opinion that various bodily characteristics are bound together has been substantiated by studies in the correlation of all sorts of organs in plants and animals and the degree of this correlation measured. This

There is also one journal devoted exclusively to biometry, *Biometrika*, published in London and edited by Pearson, Weldon, and Davenport, with the advice of Francis Galton.

index of correlation measures the degree of morphological kinship or of physiological interdependence. Symmetry gains a quantitative expression, and it is interesting to find that originally non-symmetrical organs which have secondarily gained antimeric relations — as in animals that habitually lie on one side — gain a very high index of correlation. Thus I find in the scallops (*Pecten*), which are lamellibranchs that have come to lie on the right side, the index of correlation between the dorso-ventral and antero-posterior diameters is 97 per cent, whereas the correlation between the breadths of the right and left valves is only 86 per cent. As heredity is only one phase of correlation, the inheritance of characteristics can, by the new methods, be exactly measured. It is demonstrated that there is such a thing as prepotency of one parent, and that heredity is weakened by change of sex. It is shown that mental and physiological characteristics are inherited exactly like morphological characteristics: and that the relationship between the leaves of a branch or the zoöids of a colony is like that between brothers of a family. We learn that all inheritance is not all of one kind; that certain characteristics, like stature and skin color, blend in the offspring; while others, like the coat color in mice, refuse to blend, and may be inherited according to Mendel's law.

By mathematical analysis the selection of particular characteristics, or those of a particular degree of development, has been demonstrated, and the exact effect of the selection process upon the frequency polygon has been made clear. Extreme variants are often annihilated, although in other cases the position of the mode is shifted. Finally, through quantitative studies the existence of local races has been clearly proved — the degree of their differentiation and its dependence on environmental conditions has been measured. It has been shown that a characteristic does not remain the same in all localities and under all conditions, but may become slightly altered. This fact speaks strongly for the contention that new species may in some cases have arisen by the summation of infinitesimal differences — that not all evolution is by mutation.

In concluding this address I am impressed by the fact that to-day any science ramifies in all directions toward every other. There can be no doubt that the most fruitful work in any science is to be done in the border-line between it and some other science. There is another corollary to this close interweaving of the sciences, and that is that the existing classifications have become antiquated. Our university departments, our societies, and our journals still, for the most part, draw the old lines. Yet the true work of science has, I apprehend, overleaped the barriers of these classifications, and the best workers will in the immediate future be no longer botanists, or zoölogists, or chemists, or mathematicians, but will be interested in particular subjects, — in following some favorable lead into the unknown. The embryologist who is interested in processes, the cytologist who is interested in the fertilization of the egg, will feel free to work on any material, whether plants or animals or crystals or colloidal mixtures — and by any methods that seem likely to be of aid to him. And I hope to live to see the day when our now overgrown zoölogical and botanical societies shall languish while groups of men devoted to a common subject and investigating it with the most diverse material will meet together to discuss results of common interest. When a subject no longer demands vigorous investigation, and the centre of activity is shifted elsewhere, I should like to see the old associations abandoned and new ones formed to advance the newly risen problems. Our large societies are a hindrance, I sometimes think, rather than a means of advancement to science. We want smaller meetings with more acute interest. And, finally, I cannot but remark on the vastness of the preliminary training which the present ramifications of every science make necessary. Research in the fields between the old sciences has rewards for the investigator, but he who would reap those rewards must prepare himself through years devoted to gaining the mastery of many sciences.

THE PRESENT TENDENCIES OF MORPHOLOGY AND ITS RELATIONS TO THE OTHER SCIENCES

BY ALFRED MATHIEU GIARD

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ALMOST forty years ago, on the occasion of a great international manifestation of human thought such as this in which we are convened at the present moment, in his report concerning the progress of physiology [1] presented to the Universal Exposition of Paris in 1867, the illustrious Claude Bernard tried to show that the sciences should be separated into two classes: one, including astronomy and the natural sciences, sciences of *contemplation and observation,* which should tend only toward the prevision of facts; the other, in which he placed physics, chemistry, and physiology, which alone, he said, are the *explanatory, active, and nature-conquering sciences.*

This kind of contrast established between the sciences of nature, to the laws of which we submit passively, and those in which the activity of man intervenes is the reiterated but considerably improved expression of the opinion of the philosophers of the seventeenth century, especially of Thomas Hobbes, who in his book, the *Leviathan,* expressed it in these terms: "The Register of *Knowledge of Fact* is called *History.* Whereof there be two sorts; one called *Naturall History;* which is the History of such Facts, or Effects of Nature, as have no Dependance on Mans *Will;* Such as are the Histories of *Metalls, Plants, Animals, Regions,* and the like. The other is *Civill History;* which is the History of the Voluntary Actions of men in Common-wealths."

[1] Claude Bernard, *Rapport sur le progrès de la Physiologie générale en France* (1867), p. 132, and *Revue des cours scientifiques* (1869), p. 135 *et passim.*

In conceding to the sciences of nature the power to predict facts, Claude Bernard gave them, at least in appearance, a very wide range; for what constitutes the essence of a science, as had been recognized already by Locke, is prevision of the future, and one may repeat with W. Ostwald, "The greatest leaders of man have been those who saw most clearly into the future." [1]

But if we seek to understand better the thought of the great French physiologist, we soon realize that the rôle of contemplative observer attributed by him to the morphologist is very modest in comparison with the far more exalted part which he proposes to reserve for the sciences called experimental or nature-conquering.

It is to these the duty comes at the same time to foresee the events at will and to create them at need: for the observer considers phenomena in the state in which nature offers them to him; the experimenter causes them to appear under the condition of which he is master. The naturalist is a describer; the physiologist is a creator.

Debatable at the time it was advanced, and, in fact, soon debated by men of great ability, the division of the sciences proposed by Claude Bernard was not able to resist the progress of ideas, so rapid at the close of the nineteenth century.

It rested in great part upon a misunderstanding of the conception of the word experience, to which we saw fit to give, as we shall see later on, a less restricted significance than that of the school of Magendie and of certain physiologists to-day.

Furthermore, to those who may desire to see in this discussion something besides a question of a word and a change of labels, it will be easy to reply directly by the history of the conquests due to morphological studies since the middle of the last century.

Especially in the new and so little known domain of cytology can it not be said that all that we know concerning the fundamental question of cell-division is the fruit of the efforts of the morphologists, that the methods employed by the histologists to elucidate the problem of cell-division go far beyond simple observation, and that they have required as much persevering ingenuity, as much technical skill and accessory knowledge, as any experiment in pure physiology involves?

The triumph of the doctrines of Lamarck and Darwin, the splendid intellectual movement aroused even as early as 1857 by the publication of the *Origin of Species*, the controversies of all sorts aroused by the theory of modified descent, soon began to overthrow the views of naturalists and to assign a new significance to mor-

[1] Wilhelm Ostwald, *The Relation of Biology and the Neighboring Sciences* (University of California Publications, *Physiology*, vol. 1, p. 15, Oct., 1903).

phological researches, as to the work assignable to other branches of biology.

Natural history was able in its turn to aspire to the title, explanatory and nature-conquering science. And if this transformation of opinion does not occur more promptly and more nearly simultaneously in all countries of high scientific culture, the fault is largely that of the naturalists themselves, for their obstinacy in preserving ancient dogmas, for their defiance of valuable ideas for which the authors have been ignored at first in their own country.

So long as biologists obstinately support the view of Cuvier and of R. Owen that vegetable and animal species are immutable and that the supreme end of science is classification, it is evident that the history of living beings can be only the exact description of their external form and of their internal structure in the adult and in the larval states, the comparison of these forms and of these structures, the study of the habits, that is to say, the relations of the organisms among themselves and to the environment, the distribution of these organisms over the surface of the earth considered as the result of caprice or of the intelligence of an omnipotent Creator. Outside of their practical applications (the utilization by man of animal or vegetable products), natural history yet can give enjoyments similar to those that we experience at the sight of an object of art, of a kind, however, of which the technique escapes us, and of which the results remain for us an inexplicable enigma.

But the point of view changes entirely, if in the place of considering creation in a static state as a whole, thenceforth immutable, we consider it from the dynamic point of view; if we no longer study the *natura naturata*, but the *natura naturans*, in seeking to discover the relationships of living beings, and to unravel the complicated processes by which forms and organisms are determined and related to one another; if we cease to admire devotedly the harmonies of animals and vegetables either among themselves or with the surroundings which environ them, and to hold to the childish finality of which Bernardin de St. Pierre has given us the most perfect expression; if, in a word, we abandon the anthropocentric method in order to seek to explain how these harmonies gradually became established or modified as the conditions of the environment in which they were realized were being established or modified.

Even as early, as 1877 at the congress of German physicians and naturalists which met that year at Munich, one of the first and most ardent protagonists of the Darwinian doctrine, Ernest Haeckel, could proclaim with entire justice: "By the theory of descent, biology in general, and especially zoölogy and systematic botany, are truly raised to the rank of natural history, a title of honor which they have borne for a long time, but which they merit only in our day. If these same sciences still are often designated, and that even officially as descriptive natural sciences in contrast with the explanatory sciences, this proves that a false idea exists even at present of their true significance. Since the natural system of organisms is regarded as the expression of their genealogical tree, taxonomy, so dry in its descriptions, makes a most vital place in the history of the genealogy of classes and of species."[1]

A still more important consequence resulted from these new conceptions. The theory of descent introduced into the biological sciences a unity of view, a community of end, which established among them the closest relations of mutual dependence and suppressed all futile questions of supremacy or of precedence. Indeed, whatever were the methods employed, deduction or induction, observation or experiment, anatomy, physiology, ethnology, geonomy, taxonomy, paleontology, all these parts of a whole thenceforth indivisible should tend to the realization of the same programme: to retrace in a manner as exact and as complete as possible the history of the manifestations of life upon our planet, while leaving to the metaphysicians and to the poets the business of seeking the earliest origins or of celebrating the finalities.

A hasty glance will permit us to appreciate what results have already been obtained by this concourse of converging efforts and what hopes we may conceive for the future, when, extending its frontiers, biology shall benefit by the progress of science, with which thus far it has had only too distant relations. Thus, while the old branches of morphology rejuvenated and vivified will cover themselves with a new foliation, we shall see develop about her new branches swollen with an abundant and vigorous sap: cytology, promorphology, tectology, experimental morphology (or the creation of forms by the action of primary factors), genesiology, biometry, etc.

But the very fact of the direct dependence of these different parts of the science, their mutual interferences, the complex of causes which have presided at their birth and over their evolution, frequently render this exposition difficult and at times perhaps obscure.

I may be permitted to excuse myself in advance and to claim all the indulgence of my audience if I have not always succeeded in finding the *lucidus ordo* that the Latin poet claims. You will kindly excuse me also for often having given a dogmatic and aphor-

[1] E. Haeckel, *The Theory of Evolution in its Relations with Natural Philosophy*, Congress of German Naturalists in Munich (*Revue Scientifique*, December 8, 1877, p. 531).

istic form to the propositions for all of which the evidence is perhaps not sufficient. A more complete demonstration would have required the lengthiness that I have insisted on avoiding. My conviction, too decisively and perhaps too strongly expressed, is based in every case upon mature reflection and upon the experience of long years of study.

Certainly the change of orientation introduced into the natural sciences by the transformation theory does not detract from the positive value of the results previously acquired by the purely descriptive method, and we cannot overlook the materials slowly accumulated by our predecessors. We can continue to proclaim accord in this matter with Cuvier: "La détermination précise des espèces et de leurs caractères distinctifs fait la première base sur laquelle toutes les recherches de l'histoire naturelle doivent être fondées; les observations les plus curieuses, les vues les plus nouvelles perdent presque tout leur mérite quand elles sont dépourvues de cet appui; et malgré l'aridité de ce genre de travail, c'est par là que doivent commencer tous ceux qui se proposent d'arriver à des résultats solides."

A great number of naturalists devoted to the systematic study of morphology received the idea of the variability of species with mistrust, thinking that this idea undermines the principles upon which their science of predilection rests. Events have not been slow in proving that these fears were chimerical. In order to demonstrate scientifically the reality of variations often very slight at first, it was necessary to be more precise than formerly, and sometimes even to give minute descriptions of the forms under discussion. The preservation of types in collections and museums, their graphic representation and their careful comparison with related species became more and more prominent, and certainly the advances of systematic natural history have been strongly stimulated by the disputes of the partisans and the adversaries of the theory of descent.

The study of new forms, the search for intermediate types, abnormalities, mutations, local varieties, no longer have as their sole purpose the satisfaction of a vague feeling of curiosity. The knowledge of slight modifications of structure, of slight steps in normal morphology, have become precious elements for the construction of phylogenetic trees.

Natural classification, instead of being a subjective entity, variable with the conceptions peculiar to each systematist, is now presented to the mind as an objective reality: the genealogical history of living beings of which we can already conceive a general plan, very imperfect undoubtedly, but for the establishment of which all later discoveries should coöperate.

The works of specification have a higher end, a rôle not only of description but also of prediction and origination; they rise a step in the scale of human knowledge. Their interest then becomes much more important.

And this interest is not limited to the science of beings actually living, it extends to the study of extinct forms hidden, in a petrified state, in the depths of the earth.

Paleontology opens before us as a gigantic collection of archives, and despite the regrettable gaps which the future undoubtedly will more and more fill up, it furnishes us the most precious documents for the retracing of the ancestral lines of plants, of animals, and of man himself. Veritable *médailles de la création*, the fossils enable us to reconstruct upon firm foundations the natural history of living beings in the exact sense of the word by methods analogous to those that brought into use history, properly so-called, as the sociologists and philosophers understand it.

From this moment paleontology forms with zoölogy an indissoluble whole and these two divisions of morphology reciprocally furnish coöperation. But zoölogy is incomplete. Despite the efforts of generations which preceded us we are still far from knowing all the living beings which actually exist on the surface of the earth. Paleontology has given us only very rare indications, if we consider the great number of organisms which have disappeared without leaving permanent traces (protoplasmic beings which lack a skeleton or which have a slightly resistant skeleton, etc.), especially if we think of the difficult and rarely realized conditions which were necessary to assure the fossilization and the preservation of animals through all the vicissitudes of the earth's surface. Many of these gaps in the morphological series are in course of disappearing or will disappear little by little, thanks to the more effective methods of investigation which we possess, thanks also to the progress of physical geography and to the more intensive study of the countries thus far unexplored.

Geonomy, or the study of geographical distribution, also, is greatly illuminated and simplified by the doctrines of transformation. The actual distribution of animals and plants should no longer be considered as the result of chance or of a directive principle which replaces the old creations by new ones just as one sees the scene change in the theatre each time the curtain rises.

A causal connection exists between the past and the present. Paleontology indicates to us those portions of the earth in which we should seek forms with archaic characters, and geonomy in turn enables us to divine the changes of the earth's surface and reveals to us the distant causes for the suppression of animals which have already disappeared.

But still more than geonomy, a new science or rather an exceedingly rapid development of a too much neglected branch of the science of morphology, should soon remedy the inevitable insufficiency of the actual zoölogical principles and of our paleontological knowledge.

So long as the naturalists were content to catalogue and to compare among themselves, after the fashion of a collector of arms or of objects of art, some of the many forms whose astonishing variety they admire as the fruit of the inexhaustible imagination of an infinitely ingenious Creator, it was to the adult states especially, considered as perfect, that they directed their attention. It was of little importance to them to know how the objects of their favorite passion were formed. With the exception of some rare precursors (Aristotle in antiquity, Malpighi, Swammerdam, Harvey, C. F. Wolff in a more recent period) the majority of biologists were not interested in the study of development.

Even to-day, moreover, we find among the systematists a sort of vestige of this state of mind. Among a thousand entomologists how many are there who have the least interest in the collecting of caterpillars or the larvæ of insects? Of a hundred ornithologists how many deign to admit the nests or the young of birds into their collections?

It is not the least service that the theory of evolution has rendered to biology that it has shown the importance and the necessity of embryological studies.

It is only fair to recognize that the ground was prepared by the simultaneous development of other collateral branches of science, and especially by the progress of micrography and the advent of the cellular theory.

However, we have the right to maintain that it is especially to a desire to verify in a new way the ideas of Lamarck and of Darwin that we must attribute the abundance and the perfection of embryological investigations pursued after J. Müller and von Baer, by Gegenbaur, Haeckel, Leuckart, Huxley, Loeven, Van Beneden, Agassiz, and others.

By its continuity, by the dependence of its successive phases, by the causal nexus which determines them and the relations among themselves, the development of larvæ and of embryos, or in modern language, the ontogenetic series of embryological stages is marvelously fitted to illustrate the theory of modified descent by examples which afford convincing evidence.

Undoubtedly even before the publication of the works of Darwin and the beautiful group of embryological monographs, of which we are about to speak, Serres had foreseen, by a kind of divination of genius, the fruitful idea of the transitory repetition in individual development of the forms which are permanently realized in the actual zoölogical series. But this idea could not be fully understood and bear all its fruits until it was completed and solidly demonstrated by Fritz Müller in his admirable little book *Für Darwin.*

From that time the triple parallelism existing between the zoölogical series, the ontogenetic series and the paleontological series, appeared as a necessary consequence of the phylogenetic kinship of animals, and as the evident interpretation of their genealogical relations. Furthermore, as should happen in the application of all serious theories, the apparent exceptions due to abbreviations or to falsifications of ontogenetic evolution may be foreseen and explained partly by the principles of the Darwinian doctrine: natural selection and the struggle for existence.

It is then with good reason that the principle of Serres and of Fritz Müller has been called by Haeckel the fundamental biogenetic law, if we give to this word law the meaning that we ordinarily give it in experimental sciences, that of a general formula susceptible of sufficient verification and permitting us indefinitely to predict new facts. Rich in the works of Daubenton, of Haller, of Camper, of Pallas, of Vicq d'Azyr, comparative anatomy seemed to have received from the genius of Cuvier forever indestructible foundations.

It could not escape, however, from the renovating action of evolutionary ideas. The problems that it always had in view, the questions that it apparently had answered, soon reappeared in improved forms; Huxley, Gegenbaur, Leuckart were not slow to show us in what direction definite solution was to be sought.

The pretended law of the correlation of forms (Cuvier), the principle of connections (Et. Geoffroy Saint-Hilaire), that of the balancing of organs, the idea of the degeneration of types (de Blainville), the notion of rudimentary organs, etc., instead of being simple empirical formulas, became the synthetic expression of real and necessary relations between organisms related by consanguinity, and if they had not already been firmly established inductively, these conceptions could have been deduced as the necessary corollaries of the genealogical kinship of living beings.

If we turn to the memoirs of the period and to the famous discussion between Cuvier and Et. Geoffroy Saint-Hilaire concerning the unity of organic structure, a discussion in which Goethe followed the Peripatetics with so much passion that he concentrated the strength of his mind upon it to the neglect of the political revolution which occupied every one in 1830, we recognize with astonishment that neither the one nor the other of the illustrious adversaries appreciated the much greater significance the debate would have acquired if it had taken account of the ideas that Lamarck had already supported for twenty years in the midst of the most general indifference of naturalists and philosophers.

It appears, indeed, from numerous passages of the *Philosophie anatomique*, that Et. Geoffroy Saint-Hilaire himself saw in the unity of the plan of organization merely the expression of an ideal kinship and that he attempted to explain it, as has often been done more recently, by a comparison with the successive products of human architecture destined for similar uses.[1]

From the philosophic point of view, then, there was not an abyss between Cuvier and Geoffroy. Both were creationists, but while Cuvier admitted the plurality of types (realized at least to the number of four by the Creator), Et. Geoffroy Saint-Hilaire considered the entire animal kingdom as the manifestation of a new unique thought developed according to an invariable plan in its chief lines, modifiable only in details.

We appreciate, without the necessity of insistence on the advantage, what light is cast upon this question of the plan of organization by the theory of modified descent and the study of progressive adaptations of living beings to conditions which vary according to time and place.

We appreciate also the precise and profound meaning which attaches to the previously vague notions of analogy and homology, the more recent ones of homomorphy and homophyly, etc.

The convergence of forms under the influence of ethological factors (pelagic life, parasitic life, etc.) ceased to hide the true affinities and little by little caused the factitious groups introduced by what we might call the *idola ethologica* to disappear from the purified classification.

The *idola tectologica* were more difficult to eliminate. The idea

[1] Here are a few very significant lines on the subjeet by Geoffroy: "Des rapports que j'aperçois entre des matériaux, lesquels reviennent les mêmes pour composer les animaux, de ces données qui produisent une certaine ressemblance ehez tous les êtres, tant à l'intérieur qu'à l'extérieur, j'arrive à une déduction, à une idée générale qui eomprend toutes ces eoineidences; et si je les embrasse et les exprime sous la forme et le nom d'unité d'organisation, je ne me propose par là que de traduire ma pensée en un langage simple et préeis; mais d'ailleurs je me garde bien de dire ce que j'ignore, qu'une chose serait faite avee intention à cause d'une autre? En définitive, je me erois, dans ees eonelusions, aussi fondés en raison que si, voyant d'ensemble les nombreux édifices d'une grande ville et me restreignant aux points communs que *leur imposent* les conditions de leurs existences, j'en venais a réfléchir sur les principes de l'art arehitectural, sur l'uniformité de structure et d'emploi d'un autre grand nombre d'édifiees. Une maison n'est point faite en vue d'une autre; mais toutes peuvent être ramenées intelleetuellement à l'unité de composition, ehaeune étant le produit de matériaux identiques, fer, bois, plâtre . .. . de même qu'à l'unité des fonetions, puisque l'objet des toutes est également de servir d'habitation aux hommes . . . "

Et plus loin: "Toute eomposition organique est la répétition d'une autre, sans être de fait produite par le développement et les transformations successives d'un même noyau. Ainsi il n'arrive à personne de eroire qu'un palais ait d'abord été une humble eabane, qu'on aurait étendue pour en faire une maison, puis un hôtel, puis un édifice royal. (Et. Geoffroy Saint-Hilaire, *Philosophie anatomique*.)

of organic type, so important as we have come to see, has been obscured for a long time by the imperfection of our knowledge concerning individuality or rather concerning individualities of different orders. Among the composite animals especially, such as the sponges, the hydroids, the bryozoa, the synascidians, we have for a long time attributed an exaggerated taxonomic value to the cormogenesis, that is, to the mode of grouping of the individuals, while neglecting the real relations of kinship that the anatomy of these individuals reveals. It is not the least service rendered by E. Haeckel to biological science that he first attempted to fix the rules of this branch of morphology, which is like the architectonics of living beings and which has been called tectology. Especially among the metazoa, the tectological idea of the person, that is to say, of the original diblastic being (gastrula) which constitutes the most common mode of individuality, is an acquisition of inestimable value.

Foreseen by de Blainville and by Huxley, who deduced it from purely anatomical considerations, this idea was clearly established by Haeckel as early as 1872, thanks especially to the admirable embryological investigations of Alexander Kowalevsky, investigations which proved the existence of the gastrula larva in all the groups of multicellular animals in which the development is explicit.

Despite the recent attacks to which it has been subjected, the theory of the gastrula, properly understood, is established as surely as that of the homology of the blastodermal layers which is the immediate consequence of it.

The rational application of the principle of Fritz Müller is sufficient to account for the difficulties offered by certain condensed or cœnogenetic developments and the objections presented by some authors who often hold to that which they have studied in only a very small number of types (sometimes one unique type), chosen by reason of practical convenience and without regard to the disturbances of ethological factors to which these types were subjected.

The idea of an original form common to species but often profoundly modified by the influence of environment renders evident the folly of basing comparisons upon promorphology solely — that kind of crystallography or geometry of living beings.

Such groups as those of the *Radiaria* or *Radiata*, the *Bilateralia*, etc., are purely artificial and inspired solely by the *idola promorphologica*.

The truth remains, however, that it would be very desirable to pursue further than has been done at the present time the promorphological studies of which Haeckel has furnished the basis in his admirable general morphology. In this respect, as in many others, morphology is directly dependent on geometry and mechanics. There is material for numerous problems of very vital interest for those who do not wish to content themselves with the easy but childish solution of final causes.

"Voir venir les choses," Savigny has said, "est la meilleure façon de les observer." Morphology, in brilliantly illuminating comparative anatomy, makes possible the rectification of numerous errors of taxonomy and the better appreciation of the value of different taxonomic groupings. But at the same time that they aided in the advancement of normal morphology, embryological studies, extended to abnormal forms of development, demonstrated the great influence of the science of monstrosities or teratology. Soon, thanks to the patient investigations of Dareste and to the abilities of Chabry and W. Roux in the artificial production of animals, teratology became an experimental science, and it was from that time easy to understand how in intervening in a more or less constant manner at different periods of ontogeny the cosmical or biological factors have gradually been able to modify the larval forms and indirectly the adult forms of living beings.

As a result of the science of the habits and relations of living beings either among themselves or with the cosmical environment, ethology or bionomy, somewhat neglected since the time when Réaumur, De Geer, etc., cultivated it with so much success, gains a new interest and offers to every biologist a collection of experiments prepared by nature and of which it is necessary only to interpret the results.

Is it not remarkable indeed to see the bionomy of the adult modify the development of the embryo so profoundly as sometimes to hide, in the course of evolution, the affinity which exists among related forms?

Does not the vegetable or animal diet of a mammal, for example, follow as a consequence primarily of the state of perfection at birth and also of the abbreviation of the embryological processes, since the young are not sufficiently protected by their parents, whose rapid movements in search of nourishment or for the avoidance of an enemy they must follow?

The animals which are fixed in the adult state, and especially parasites, which early establish themselves upon the host and never leave it, necessarily have an explicit development, and the motile larvæ are provided with organs of sense which permit them to choose with care the resting-place where the greater part of their existence will pass. On the contrary, in pelagic beings, which early in life are exposed to a thousand dangers, there would be every reason why the progeny should be protected by direct, rapid and cœnogenetic development or be trusted to a strange nurse, as is the case with the copepods of the group *Monstrillidæ*. Even evolutionary phenomena as complicated as those in the *Coleopteran, Meloïdes,* under the name of hypermetamorphosis, become easy of explanation if we view them in their relation to bionomic conditions and as a necessary consequence of the life which their ancestors had to lead.

Not less interesting, it seems to me, are the embryological peculiarities that I have brought together under the name "*poecilogonie.*" Two beings belonging to the same species as like as possible in the adult stage, so much alike sometimes that the eye of the best-trained specialist cannot detect the least difference between them, may present in the series of their ontogenetic stages and even in the ovarian form very marked differences, if their embryonic bionomy is not the same; if, for example, the environment has not the same chemical composition or if the season of development is different, or yet again if the biological conditions vary with the cosmic surroundings in the different habitats of a widely dispersed species, whence the terms *poecilogonie géographique*, *poecilogonie saisonnière*, etc.

What is more astonishing than these curious experiments of morphology realized by nature, which I have formerly discussed under the name of parasitic castration? And however mysterious the modifying action of the indirect *gonotome* may be to us, is it not very instructive from the morphodynamic point of view to see this parasite, by action at a distance upon a host of determined sex, cause the appearance of the characters of the opposite sex even when these characters will have no value for the animal which possesses them? Finally, this notion of a morphological complex constituted by the host and its parasite acquires primary importance when we relate these parasitic complexes to the unstable biological equilibrium of homophysical or heterophysical complexes in more or less permanent equilibrium, realized either in the galls or in symbiotic forms such as the lichens, plants with mycorhiza, etc.

At most the notion of complexes of different beings associated in harmonious symbiosis is only a generalization of what we observe in all multicellular organisms in the course of their evolution.

As early as the middle of the eighteenth century C. Fred. Wolff had established upon a firm basis the theory of epigenesis. He showed that living beings do not develop, as had been thought, at the expense of a preformed rudiment, growing much as the image of an object enlarges when examined successively with glasses of gradually increasing powers of magnification.

The different organs of an animal are formations of a relative autonomy which work together in the construction of a whole whose equilibrium is not preëstablished and whose plan may sometimes be modified during the course of construction.

It is well understood that in respect to reciprocal dependence the different systems of organs vary considerably. Sometimes this dependence is very close, as when the appropriate functions of the organs are themselves very closely united, respiration and circulation, for example. It can be much less close when it acts with reference to parts adapted to very distinct rôles, organs of locomotion and the digestive apparatus, or better the tegumentary system and the skeleton, etc.

But the independence is especially great if we consider on the one hand the organs which subserve the life of the individual and on the other those which are destined to insure the perpetuation of the species.

The soma and the gonads, to employ modern expressions which designate these two totalities, are in a certain sense two organisms, which are juxtaposed or incased the one in the other, whose development may proceed very unequally, although any modification effected in one has in general an influence upon the other.

It is because of their reliance upon this notion fundamentally exact, but exaggerated and enveloped with a metaphysical atmosphere, that the partisans of the ancient theory of evolution (preexistence and germinal localization, preformation of the embryo) have for a long time struggled against the ideas of C. F. Wolff.

In following the same line of thought more recently, A. Weismann has sought to construct his well-known theories upon the assumption of the non-transmissibility of acquired characters.

Finally, it is the same consideration which, when extended to the first phases of embryology, to different cellules of the morula and even to different regions of the unsegmented egg, has served as the basis of the mosaic theory of W. Roux, which has since been so ingeniously modified by E. B. Wilson.

While adhering to the strict observation of facts easiest to verify, we shall call only that epigenesis which, in revealing to us the possibility of a vital concurrence between the organs and even between the plastids which constitute multicellular beings, permits us to explain easily all the complex facts of evolutionary polymorphism; progenesis, *néoténie, dissogonie, poecilogonie*, and in general the curious peculiarities of development that since Chamisso and Steenstrup we have grouped under the very improper name of alternate generations or of geneagenesis (de Quatrefages).

There is thus established a vast array of information which is sufficiently extended to constitute to-day a new branch of morphology which we may call genesiology.

The object of genesiology is the study, both descriptive and experimental, of different evolutionary modes.

In the preceding pages we have at different times spoken of experiments and of the experimental method in a sense different from that which is often given to these words by the physiologists of the old school. This is the place perhaps to indicate the manner in which we understand the introduction of experimentation into the morphological sciences and the results which may follow for the later development of these sciences.

An experiment always necessitates the preliminary analysis of the phenomena by which the fact that one wishes to observe and if possible to measure is conditioned. It assumes a hypothetical solution of which it will show the reality or the non-existence. Every experiment is then preceded by an induction and followed by one or more observations. The experimental method is always, as Chevreul called it, a method *a posteriori.*

Experiment creates nothing; it has precisely the same value and the same logical significance as the proof of a mathematical operation.

For an experiment it is not necessary to demand, as some seem to believe, a complicated plan, a richly equipped laboratory and costly apparatus.

It is necessary indeed not to confound the precise measure of a phenomenon which often is obtained by the aid of very delicate instruments with the pure and simple establishment of a causal relation between one fact and the other facts which determine it, an establishment which is the basis of the experiment itself. Even if the fact were accidental, as the fall of the apple before the eyes of Newton, its determination may nevertheless become an experiment. And it is only the mind of the observer which will give it this character.

> Das ist ja was den Menschen zieret
> Und dazu ward ihm der Verstand
> Dasz im innern Herzen spüret
> Was er erschafft mit seiner Hand.

Where the unscientific person sees without interpreting and takes a purely contemplative attitude, the naturalist worthy of the name supplies the supposition of voluntary acts the action of whose factors he wishes to study.

An animal receives in the hunt or by some other accident a ball in the left side of the neck; the right side is paralyzed. If the fact is well determined and freed from all cause of error its voluntary reproduction in the laboratory would be only the verification of an experiment already realized.

Not only does nature at present offer us, as we have said, numerous experiments, many of which are very difficult to repeat, but we may also say that paleontology furnishes us experimental data of incalculable value. The arguments which it furnishes to transformational morphology are not, as is sometimes pretended, purely conjectural; the degree of certainty that they possess is not inferior to that in astronomy or in the other divisions of the physical sciences whose objects are partly inaccessible to us.

Hilgendorf and Hyatt studied the different layers of the tertiary lake of Steinheim in Wurtemberg. They recognized that certain forms of *Planorbis* differing little among themselves in the deep layers (the oldest) [1] are separated little by little from one another, and finally, in the most recent layers, constitute species as reliable as any of those described in this genus of mollusks.[2] Is this a work of pure contemplation and description? Is it not manifest that the authors have reconstructed in their thought a gigantic experiment, and if they have not in their power the complete determination of this experiment, do they not at least possess sufficient elements to infer the evolution of the forms without determining the factors of this evolution other than the time-factor, the action of which is unexceptionable in this instance?

Clearer and still more evident and in any case more in line with current ideas is the application of the experiment in the study of the Lamarckian or primary factors of evolution (cosmical factors, ethnological, etc.) [3]

Indeed it is especially by a return to the ideas of Lamarck that transformationism should cause morphology to progress more rapidly in the experimental path.

Certainly the conceptions of Darwin were in many respects justified by experiment, even in the strictest sense of the word, and Darwin has proved it himself by his beautiful investigations concerning self- and cross-fertilization and concerning climbing plants and carnivorous plants, etc. But it is necessary to recognize how many experimental verifications relative to natural selection, to heredity, demand conditions rarely realized, a length of time which renders them easy of accomplishment only by a group of persons (societies of scholars), or necessitate large resources which most investigators cannot command.

Apart from some brilliant exceptions concerning whom we shall have occasion to speak later, the disciples of Darwin who have followed most closely the tendencies of their master have understood experimentation in the very large sense that we give to this word as applied to a great number of investigations relative to secondary factors.

The importance of the study of primary factors in evolution did not escape Darwin, but, excellent observer though he was, he was

[1] The four oldest forms were the uncertain varieties of the same species: *Planorbis laevis*.

[2] *The Genesis of the Tertiary Species of Planorbis at Steinheim*, *Proceedings* of the Boston Society of Natural History, 1880; and *Transformations of Planorbis at Steinheim*, *American Naturalist*, 1882, p. 441; also Stearns, *Proceedings* of the Academy of Natural Sciences, Philadelphia, 1881.

[3] To convince us of this, it is only necessary to examine the two beautiful volumes recently published by C. B. Davenport under the title, *Experimental Morphology* (New York, 1897–99), in which we shall find an excellent résumé of what has thus far been attempted in the study of the primary factors.

undoubtedly dismayed by the complexity of the rôle of these factors and did not attempt to disentangle the mechanisms which give rise to the numberless variations of living beings.

These variations exist. He indicates them, and, without referring them to their immediate causes, attempts first of all to show that they may be so determined as to constitute races, then new species.

Darwin had read Malthus; he recognized the law of a division of labor borrowed by H. Milne-Edwards from political economy; he found that the method of the sociologists was good, and that in a science which was complicated and still young, as was biology, one might employ the methods in use equally in meteorology, in statistics, etc., in resting upon the law of great numbers without seeking to discover distant causes and to penetrate to the essence of the phenomena.

Thus he showed the importance of selection for the fixing of acquired characters when they offered some utility in the life-struggle and thus assured the survival of their possessor through a better adaptation.

But he did not seek to establish in each particular case the exact determination of the appearance of indifferent or advantageous varieties. Perhaps he was deterred from this path by the failure of his eminent predecessor, Lamarck, in the energetic effort which he had made to explain in terms of surrounding conditions (acting directly or indirectly by the creation of new needs) the gradual modifications of living beings and the transformation of species.

We must not forget, also, that at the outset of the nineteenth century, and even at the moment when the *Origin of Species* appeared, the state of the physical and chemical sciences did not permit of successful approach to most of the problems of external physiology, the search for the solution of which had been important: chemical investigations determining variations of color, the influence of different kinds of radiations, the morphogenic action of saline solutions, of osmosis, etc.

However satisfactory they may have been for the mind, and despite the enormous progress that they had wrought in morphology, the ideas of Darwin began to appear insufficient; we may even believe for a moment that the exaggerations of some of the disciples of the master merely compromised the triumph of the doctrine and led thought back toward the finalistic explanation of the ancients, now learnedly resuscitated under the name of neo-vitalism. The words natural selection, mimicry, convergence, heredity, and others like them, which in the thought of Darwin had only a provisional value, became for the philosophers and even for certain biologists, convenient formulas which served to mask the ignorance in which we most frequently find ourselves in regard to the immediate cause of variation.

Nevertheless, when in 1880 he published his very suggestive little book, *Die Existenzbedingungen der Thiere*, Carl Semper already attempted to lead back the naturalists to the study of primary factors. To the experiments of rare precursors concerning the morphogenic influence of change of alimentary regimen (Hunter, Edmondstone), of the modifications of salinity of the water (Smankevitch), of heat, of light, etc., he added original researches concerning the best conditions for crossing and for the reproduction of *Limnaea*, and especially he brought together into a volume which, although limited, was very complete in its content for the period, an enormous mass of biological observations, many of which have exactly the same demonstrative value as the best laboratory experiments. Since then, investigations of this sort have been undertaken with enthusiasm on many sides and especially in America. The impulse is given and we may rest assured that the movement will increase in force as the parallel advances of physics and chemistry permit of the application of greater precision in these studies and of access to certain questions which up to the present seemed inaccessible.

The opening-up of new scientific fields such as physical chemistry and bio-chemistry will soon furnish us means for taking up successfully the work which Lamarck was able to trace only in its general outline.

The dependence of morphology in its relation to the physical and chemical sciences is still more manifest in that branch, so new and so full of promise, which we know under the name of cytology.

Although the cellular theory, already sketched by Malpighi, had been completely formulated by Raspail (1835) and by Schleiden (1838) for plants, then by Schwann (1839) for animals; although Virchow about the middle of the last century had proclaimed his celebrated aphorism *omnis cellula e cellula*, it is only during the last twenty years that cellular morphology and cytology have attained a wonderful development, thanks to the investigations of Van Beneden, of Strasburger, and of a brilliant group of young biologists.

The history of this magnificent structure, its general plan and its details, have been very exactly retraced in a work already classical, *The Cell in Development and Inheritance*, published as early as 1896 by E. B. Wilson, one of the able investigators who with O. and R. Hertwig, Boveri, Maupas, Guignard, etc., have most actively contributed to its construction. But how laboriously this difficult work has been prepared by the numerous improvements of microscopical technique due to Leydig, Ranvier, to Max Schultze, to Flemming, etc.

And these improvements in their turn have been made possible of attainment by the advances of chemistry and especially of the chemistry of dyes (the anilin dyes in particular). Despite the empirical and crude way in which we make use of each new conquest of the physical and chemical sciences, despite the existence of methods, which are still imperfect, such as those of Golgi, of Cajal, and of Apathy, what morphologist would be blind enough to deny the importance of the new data which we owe to technical processes of which the theory is very often unknown to us? But chemistry has rendered us services not less important in enabling us to penetrate into the finer structure of the chromatin substance and of the albuminoids in general. In this fruitful way, which Robin had already attempted, but which has been opened to us by Schutzenberger and by Kossel, cytological morphology will certainly find the key to many of the enigmas which arrest it at the present time. And what progress shall we not be able to attain through the chemistry of colloids of which our present chemistry is, in a fashion, only a special case.

That cytological morphology should be contributed to equally and in large measure by physics and especially by optics, is too evident to be necessary to insist upon. I desire only incidentally to make a remark which will show what influence scientific studies which are very dissimilar in appearance may have upon one another.

There is no doubt that the perfecting of micrographic apparatus, and especially of immersion objectives, has been due in such large measure to the desire of the constructors to satisfy a clientage which is special and sufficiently large in certain countries, namely the collectors of diatomes, that these amateurs, sometimes unjustly disdained by those who wish to establish air-tight partitions between scholars of different orders, have indirectly rendered great service to pure histologists and to those who study the most delicate problems of cytology and of cytogeny.

The bacteriologists, while aiming at a very different and much more practical goal, have contributed still more than the diatomists to the perfecting of our micrographic equipment in extending to a new class of investigators, the pathologists and clinicians, the daily use of the microscope.

And in this domain of pathological anatomy we again see produced these very fruitful interactions with the science which more especially interests us. The study of tumors, cellular teratology, at the same time that it is illuminated by the facts of normal cytology, furnishes us with very suggestive views concerning the significance of chromatin reduction and of its unexpected connections with the new phenomena of the first embryological phases (Borel, Moore, and Farmer).

The idea of phagocytosis, studied by Haeckel in the biology of the protozoa, by Rouget in the examination of the leucocytes of the blood, increased in value and importantly developed by Metchnikoff, who made many applications of it in the domain of pathology, has come by a most fortunate turn of events to elucidate certain of the most obscure of the morphological phenomena of embryology, the cœnogenetic processes of ovogenesis and of metamorphosis.

For a long time the introduction of the mathematical sciences in the domain of morphology has been regarded with suspicion; it seemed dangerous indeed to wish to bind by very simple formulæ facts so complex as those studied by zoölogists and botanists.

Little by little, however, the necessity of determining by precise measures the extent of variations due to primary factors and of seeking to find the laws of these variations has made itself felt. Among the first Delboeuf attempted not without success the application of algebra to the problem of the formation of races. But it is especially to Galton and to his school that the most important of the works of mathematical biology and biometry are due.

Whatever be the character to which we give our attention, if we consider a great number of specimens of a given species we recognize that the individual variations (continuous or fluctuating variations) of this character, numerically expressed, do not exceed two extreme limits which are reached by a very small number of the individuals. Between these two extremes there is a constant mean variation with the greatest number of observed specimens. It results, that if we take as abscissa the lines which represent the extent of the fluctuations and as ordinates the distances corresponding to the number of individuals which present a certain fluctuation, we obtain a curve which Quetelet called a binomial and which is in reality only a curve of probable error. We also often give to these curves the name Galton's curves, because of the very extended use that this eminent biologist made of them in the study of the question of heredity.

By artificial selection breeders and horticulturists succeed in displacing more or less rapidly the apices of the Galtonian curves and in directing fluctuation in the way they desire. Natural selection does not operate otherwise for the modification of the form of species and it is to this action that Darwin attributed in great part the transformation of species.

Wallace, more especially, considered selection as the sole factor determining the evolution of living beings.

It was reserved for Hugo de Vries to show through long and delicate cultural experiments, the exaggeration into which the immoderate disciples of Darwin (Romanes, Weismann) had fallen.[1] Guided by his earlier studies concerning the Galtonian curves and impressed with the constancy of certain forms, such as the species described by the botanist Jordan, whose origin was difficult to explain by fluctuations, De Vries supposed that after periods of relative fixity during which they are subject only to fluctuating variations, living beings may pass through shorter periods when their forms are abruptly modified in different directions by discontinuous changes.

Biologists clearly recognized this kind of variation in what they call sports. De Vries has called them mutations and he has shown the importance of mutability especially in the study of a biannual plant, *Œnothera Lamarckiana*, an American species introduced into Europe, especially into many localities of the Low Countries. From 1880 to 1899 each year De Vries has planted in the botanical garden at Amsterdam from 15,000 to 20,000 seeds of this plant. Besides thousands of normal individuals, his cultures have produced seven new types, represented each year by a variable number of individuals and capable of reproducing themselves by seed with great regularity. Among the 50,000 *Œnothera* plants that he has observed during ten years De Vries has counted 800 that might legitimately be called *Œnothera Lamarckiana*, but which are divided as we have just said into seven groups, to which it was fitting to give the systematic value of subspecies, as the botanists would not have failed to do if these plants had been found in the fields where their origin was not known.

A great number of biologists have believed that they found in the splendid studies of De Vries unanswerable arguments against the theory of selection. It is impossible for me to share their opinion. I should say even that in examining the question closely and in penetrating to the bottom of the matter, it is impossible for me to find in the theory of mutations anything except a useful complement of the Lamarckian and Darwinian doctrine of continuous variation.

As the economist Bastiat has said, in all complex phenomena where multiple causes intervene in different ways, there is that which we see and there is also that which we do not see.

What we see in a mutation is the abrupt and sudden appearance of a character which did not previously exist, but this character is only the sudden manifestation of a state which has been prepared very slowly in the ancestors of the individuals in which it appeared. In order to obtain a chemical reaction, in order to cause the color of a liquid to change, it is often necessary to add the reagent drop by drop, until an instant when all at once the reaction occurs and the new color appears. The mutation is the result of a new state of equilibrium in the varying organism. All the individuals in which this new equilibrium appears are in a different state internally from that of their

[1] H. de Vries, *Die Mutationstheorie*, Leipzig, 1901–03.

ancestors, they are in internal fluctuation and it is this that we do not see.[1]

If modifications should be produced in the veins of an insect's wing, for example, it is impossible that these modifications should express themselves otherwise than by a new mechanical disposition constituting in relation to the preceding a sudden variation in the disposition of the cells and of the veins. In the same way, the appearance of a new vertebra or of a new metamere in an animal whose metamerism was fixed could occur only in discontinuous fashion and not by infinitesimal fractions of a vertebra or of a metamere. The fact that mutations always appear in limited number (seven in the case of *Œnothera Lamarckiana*) shows clearly that a certain number of positions of equilibrium are in question, among which there are no realizable morphological transitions, and of which some seem difficult to obtain. Of the seven species of *Œnothera*, a single one, *Œnothera gigas*, has proved robust. The others are for the most part very weak, and demand much care in order to flower and to mature their seed. Often, indeed, there are only two possible equilibriums; this is true in the case of dimorphism or ditaxies of colors, to use the language of Coutagne, so common in plants, in mollusks, in the lepidoptera, etc.

In reality, as I wrote a dozen years ago, while fluctuations may be compared to gradual oscillations from one side to another of a mean position, mutations represent so many states of stable equilibrium among which continuous passage cannot be established. The intermediate forms of these states of equilibrium are not explicitly realized because they do not correspond to sufficiently stable states. The following trivial comparison will serve to render my thought easier of apprehension: we cannot rise a half or any fraction of a step of a stair. In such cases progress is necessarily discontinuous, or, what amounts to the same, is manifested only in a discontinuous manner. But we cannot adduce from these facts any argument against the formation of species by natural selections; there is all the more reason why it is not necessary to seek the unique and complete solution of the very complex problems of transformation.[2]

[1] A botanist whose original researches concerning variation in plants have not attracted sufficient attention, A. T. Carrière, made an ingenious comparison in this connection:

"Nous pouvons," he says, "afin de nous représenter le double effet, l'effet lent et l'effet brusque sous lequel se montre le dimorphisme (ce que nous appellérions aujourd'hui une mutation ditaxique) supposer une horloge à secondes dont on ne verrait que le cadran. Dans ce cas, l'effet continu mais lent, nous serait représenté par le balancier, qui, bien que nous ne le voyions pas, ne s'arrête cependant jamais, et l'effet brusque ou intermittent par chaque saut que feraient les aiguilles, saut qui est la résultante d'une action incessante tellement lente qu'elle n'est point appréciable à nos sens et qui ne se manifeste d'une manière sensible que lorsqu'il y a une certaine quantité de force accumulée." A. Carrière, *Production et fixation des variétés dans les végétaux, Revue horticole*, note 42, p. 71, Paris, 1868.

[2] A. Giard, *Sur un exemplaire de Pterodela pedicularia L. à nervation doublement anormale, Actes* de la Société Scientifique du Chili, IV, p. 21, 1895.

Besides, as Darwin has never denied the existence and the importance of mutations, which he called single variations, so from his side De Vries has never sought to destroy the theory of selection.

Instead of operating slowly upon fluctuating individuals, it acts upon species in process of formation. The struggle for existence exists among mutations and among the forms from which they proceed, as W. Hubrecht has very correctly observed in the clear analysis that he has recently given of the ideas of his compatriot: "Far from having undermined Darwin's Darwinism, De Vries has completed, purified, and simplified it," and only those think otherwise who combat Darwinism for other than scientific reasons, and at the bottom of their hearts wish much evil to the demonstrations of De Vries and to all other possible forms of the theory of evolution.[1]

Another interesting application of mathematics to the morphological sciences is presented by the study of hybrid forms. The laws of Mendel, recently verified by De Vries, Tschermak, Bateson, etc., carry the calculus of probability to the furthest limit. It will be useless to insist longer upon the numerous and important problems relating to morphological heredity whose solution depends on the rational study of numerical data which are as numerous as possible.

From all of these considerations we deduce at present a conclusion of remarkable generality; to wit, that the natural laws of evolution seem to enter into the movement toward physical laws which has manifested itself for some time. They assume more and more the character of static laws. Thus guided by the conducting line of the theory of descent, subjected to the precise measure of a perfect mathematical exactness, and controlled at each instant by the experimental method, morphology each day becomes more the explanatory science *par excellence* of the world of organized beings. Morphological phenomena are the translation, the tangible expression, the perceivable criterion of physiological experiments, and the latter borrow all their interest from the morphological manifestations which they engender.

In connection with breeding and horticulture the morphologist becomes in truth a creator. He is still more so when, in calling up and grouping in thought the conditions under which living beings are successively formed in the course of centuries, he perceives the causal nexus which connects the new forms with those which have

[1] "I have purposely insisted on these points, because here and there a tendency seems to prevail to look upon Darwin's views upon the origin of species as unsatisfactory and obsolete and to proclaim the necessity of replacing them by broad new hypotheses with which the name of De Vries should be coupled. These tendencies are in great favor with those that bear a grudge to the so-called Darwinism for other than scientific reasons, and who in their innermost hearts would at the same time like to see a similar fate reserved for De Vries's demonstrations, and even for the whole theory of evolution." A. A. W. Hubrecht, *Hugo de Vries's Theory of Mutations* (*The Popular Science Monthly*, July, 1904, p. 212).

preceded them, and foresees to a certain extent the transformations, undoubtedly less extended, which the forms, still possessed at present of a certain plasticity, will undergo in the future.

At all events, in pretending that the morphologist plays the rôle of creator, we do not intend to affirm that he could, as the adversaries of the evolutionary theory have sometimes demanded with ridiculous unreasonableness, transform *hic et nunc* one animal species into another species through a simple modification of food and medium, and, for example, produce the ox from the sheep by placing the latter for some generations in especially favorable conditions. Such a result would be the negation of the Darwinian doctrine itself, which, we know, makes great use of modifications accumulated by heredity and irrevocably fixed in definitely established organisms.

What the morphologist is able to attempt, and what in fact he does attempt, is to discover and to analyze the small variations which are determined by primary factors, and to determine thus how by a slow summation these variations, at first insignificant, are united to give origin, either by a continuous or by an apparently discontinuous process, to the much more evident characters which separate species.

I do not dare even to believe, with some bold pioneers of modern science, that the most perfect knowledge of the auto-regulation of organisms will perhaps permit us to modify these auto-mechanisms and to obtain thus a rapid variation of animals and plants.[1]

After a series of innumerable transformations of which it is sometimes possible to discover some traces in the form of fossil impressions in the depths of the earth, the majority of living beings have arrived at a relatively stable state of equilibrium. They have exhausted the possibilities of what I have called their plastic potential, they are able to effect only feeble oscillations about a mean position, and no considerable change in the ethological conditions, in general, can be compensated for by a new arrangement of regulative reaction.

And even for those which still have a reserve of plasmatic elasticity sufficient to permit of new adaptations, we must not forget that they can develop only in a certain number of well-defined directions, and that we must always bear in mind two essential facts which regulate the transformations which are hereafter possible:

[1] "So far as I am aware no one has yet found a method of bringing about a rapid variation in animals or plants. I am inclined to believe that this failure is at least partly due to the existence of mechanisms of regularisation. . . . We again meet with two possibilities: we shall either succeed by a series of continued slight changes in one and the same form in bringing about a large transformation from the original form, or we shall obtain the result that in each form the possibility of evolution is limited, and that at a certain point the constancy of a species is reached." J. Loeb, *The Limitation of Biological Research* (University of California ublications, *Physiology*, vol. I, no. 5, Oct. 1903).

first, the indestructibility of the past; second, the irreversibility of evolution.

It is there, we may say in passing, that all the difficulty of the question of spontaneous generation or abiogenesis lies. If by a miracle we should happen to produce from non-living material as simple a living being as can be imagined, this new being would certainly be different from all actually existing species, for the latter have a past that the other would not have, and they bear in their organism, which may be as rudimentary as we choose, traces of all action to which their ancestors have been subjected.

We may even infer that the hypothetical monads whose formation we might bring about by abiogenesis would differ from those which have originated at other times by the same process. Besides the fact that the environmental conditions in which they appeared would necessarily be different, the complexes of organic materials which would serve in their formation also would have their history, and everything leads us to think that the properties of inanimate bodies, as those of living beings, are to a certain extent functions of their antecedents.

Thus is explained why even to-day there exist very old living forms which are not developed because they no longer have available plastic potential, and which would perish before they would undergo transformation.

Thus is explained why it is vain to hope through special environmental conditions to raise relatively inferior forms of life to a higher level, and why it is useless to seek to modify physically or morally in a desirable sense races which are considered rightly or wrongly as relatively inferior, but in any case otherwise differentiated. Evolution is not reversible, and we cannot by any process cause a living being to return toward the point at which it was separated from its original phylum in order to make it follow a different way from that which it had at first taken.[1]

But the limits imposed upon our science by nature should not hinder us from admiring its grandeur and from noting its prodigious development.

It is never necessary to doubt progress. It is almost thirty years since, in the course of a lesson on the first phases of development of the animal egg, I said, not without regret: "La Morphodynamique

[1] The generality of the pœcilogonic process shows the instability of evolution. For according to Brillouin, irreversibility is introduced into rational mechanics with instability. Irreversibility, which is the almost universal character of natural phenomena realized in finite time, is by no means an objection to mechanical explanation (mechanics of the nineteenth century or the more general mechanics which caused us to discover electromagnetism) of the physical-chemical world. Wherever we actually introduce it in order to come to an issue in a numerical theory, of viscosity or of friction, a most profound analysis will cause the recognition and study of the instability of molecular equilibrium. (Marcel Brillouin, *Notices sur les travaux scientifiques*, pp. 19–20, 1904.)

soupçonnée par Lamarck, à peine abordée par quelques rares biologistes, est un territoire scientifique que la plupart des naturalistes de nos jours ne verront que comme Moïse vit la Terre promise seulement de loin, et sans pouvoir y entrer." [1]

My hopes have been greatly surpassed by reality. Under the name of embryological mechanics (*Entwicklungsmechanik*), and of biomechanics, of biometry, etc., the new fields toward which I directed my course of scientific exploration at the beginning of my career have been partly recognized and opened up by young and able investigators. Scientific progress follows a geometrical progression, of which the ratio increases unceasingly. As a river, with its impetuous waters increased by the contributions of numerous tributaries whose synthesis it effects, morphology majestically deploys its course, and the delicious æsthetic experience that the contemplation of living beings procures us is the least recompense of of our troubles and of our persevering efforts.

For the realization of a work of art, what anonymous collaborators come to the assistance of a painter or a sculptor! The artisan who weaves the canvas, the quarryman who furnishes the stone, have their share of merit in the final result, and we owe them also a share of the recognition. It is the same in our sciences of nature. where each day brings an increasing solidarity among all the workers. The different branches of biology are united among themselves, as we have seen, by multiple and intertwining bonds, and a special branch such as morphology depends not only on the progress of neighboring branches, but also on the development of other sciences, even those which are apparently most distant.

Specialization, which perforce becomes more and more intense, also renders the more desirable synthetic efforts and the coördination of results.

Let us hope, then, that in the near future a collective organization may replace the anarchical state which exists at present, and which uselessly absorbs so much activity which might be better employed in bringing the various sciences into a hierarchy and directing them toward a common end. Scientific solidarity should be the preface and the model of social solidarity.

[1] A. Giard, *Cours de Zoologie* (*Bull. sc. Fr. et Belg.*, t. VIII, p. 258), 1876.

SHORT PAPERS

PROFESSOR C. JUDSON HERRICK read a paper for DR. C. S. HERRICK of Granville, Ohio, on the "The Dynamic Character of Morphology."

The speaker said in part: There is a price which any organism must pay for a high degree of specialization in a single direction. The liver fluke of the sheep depends for the perpetuation of its species upon a series of complicated adjustments to various environments, the failure of any one of which is fatal. Such cases of extreme adaptation are usually found only on the terminal twigs of the phyletic tree, and it has come to be a biological truism that the main line of evolutionary advance passes through the generalized types.

Perhaps something similar holds true for scientific disciplines. There is certainly danger that extreme development of any specialty may cut it off from the vital relations with environing fields upon which its continued existence depends, and the elaboration of a "pure morphology" is certainly not exempt from such a danger.

But we have only to be true to our own traditions to enable us to retain our place in the growing axis of biological progress. Anatomy, out of which morphology grew up, belongs to the most static group of the descriptive sciences. But morphology is not the description of form; it is the explanation of form, and from its inception has been quickened by genetic and functional motives.

Morphology is one of the most dynamic of all the sciences; from the start it has been morphogenesis, and the key to the problems of structure is *behavior*. To draw another illustration from my own specialty, comparative neurology and comparative psychology have joined hands in wedlock from which we trust there is henceforth no divorce, and we trust not without hope of offspring.

So long as morphologists have sufficient breadth of view to assimilate the relevant data from all other sciences, there is small danger of our science becoming specialized to death, however minute may be the subdivision of our problems and however extreme may be the refinements of our methods. But isolate morphology, and it will perish.

The present problem of our specialty, therefore (if we may single out one as preëminent), is, as it always has been, *the relation of morphology to other sciences.*

PROFESSOR J. G. NEEDHAM, of Lake Forest University, presented a paper on "The Contribution of Animal Morphology to Education," in which the speaker said in part:

Two phenomena of great importance accompanied the early development of animal morphology:

(1) The general recognition of the principle of evolution.

(2) The general introduction of the laboratory method in zoölogy.

The first profoundly affected every department of human knowledge: the second profoundly influenced the development of every branch of biological science.

These were the necessary — not accidental, nor even incidental — accompaniments of the development of animal morphology: for when the theory of natural selection offered the first satisfactory explanation of a possible method of evolution zoölogists were quick to recognize that the facts of the structure and development of animals offered a ready means of testing its validity. The distinguished comparative anatomists of the first half of the nineteenth century, and the rising school of embryologists, had prepared the way: and the early morphologist found at hand structural data of great diversity and in great abundance, awaiting a new interpretation. They took the "natural system" of the old comparative anatomists, and breathed into it the breath of life. In so far as it was natural its naturalness lay not in association of like forms, but in kinship. Homology came to have a new significance, and phylogeny and ontogeny came to the fore; and enormously productive researches began into the correspondence in development of race and individuals. It is not too much to claim that the general and prompt acceptance of the idea of evolution is due primarily to the work of morphologists.

That which belongs to general intellectual culture of the race belongs to the curricula of the schools. Among the early morphologists were some eminent educators, who were not slow to recognize the great pedagogic value of the materials in their hands. They were the first among zoölogists to reduce their materials to satisfactory pedagogic form. While perhaps they did not create the laboratory method in zoölogy, they made it general. While other phases of zoölogy are likely to receive, and are worthy of more attention than they receive at present, the materials of morphology will always be of the highest general pedagogic value because they so well illustrate the commoner phenomena of evolution, division of labor, specialization, progressive and retrogressive development, redundancy and reduction of parts, parallelisms and divergent lines of development, etc. To me it seems doubtful if these phenomena, which belong to evolution in every field of knowledge, are demonstrable in any other field with such definiteness and economy of time and satisfaction as in this one. Therein lies the chief pedagogic utility of the materials of morphology.

A TRAGEDY IN THE HAREM

Photogravure from a Painting by Pierre Louis Bouchard.

An uprising in a harem is not so rare that the polygamous chief can afford to ignore such a possibility; so, to intimidate the unfortunate inmates he inflicts the most terrible punishments for violations of fidelity or attempt to escape. In the painting here shown the artist has pictured a terrible scene, in which an uprising of the enslaved wives is discovered by the concealed husband, who has summoned his mutes to seize the women, one of whom has fainted as the drawn drapery from an alcove reveals the presence of her cruel lord. The picture is full of action and Oriental richness, but almost terrifying in its illustration of customs that flourish in Mohammedan countries. This painting, which is one of Bouchard's masterpieces, has become famous in France as *Les Muets du Sérail*, and was originally exhibited in the *Salon* of 1887.

SECTION H — EMBRYOLOGY

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(*Hall* 9, *September* 23, 3 *p. m.*)

CHAIRMAN: PROFESSOR SIMON H. GAGE, Cornell University.
SPEAKERS: PROFESSOR OSKAR HERTWIG, University of Berlin.
PROFESSOR WILLIAM K. BROOKS, Johns Hopkins University.
SECRETARY: PROFESSOR T. G. LEE, University of Minnesota.

THE Chairman of the Section of Embryology was Professor Simon H. Gage, of Cornell University, who opened the Section with the following remarks:

"In this great International Congress of Arts and Science, it is peculiarly fitting that one of its sections should be devoted to embryology, that branch of biology which has to do with the unfolding and development of the egg into a complex and independent organism. We are fortunate in having for our chief speakers men — one from the old world and one from our own country — who have taken a leading part in our generation in discovering and expounding the processes and laws of development and the relations of organisms from parent to offspring in an endless chain."

ADVANCES AND PROBLEMS IN THE STUDY OF GENERATION AND INHERITANCE

BY OSKAR HERTWIG

(*Translated from the German by Dr. Thomas Stotesbury Githens, Philadelphia.*)

[**Oskar Hertwig**, Regular Professor of General Anatomy and History of Evolution since 1888; and Director of the Anatomical-biological Institute since 1888, University of Berlin. **b.** Friedburg, Hessen, April 21, 1849. Student of Medicine, Jena, 1868; Zurich, 1869; Jena, 1870; Bonn, 1871–72; M.D. Bonn, 1872; Ph.D. Bononiensis, 1888. Privy Councilor of Medicine, 1897; Regular Professor of Human Anatomy and Director of Anatomical Institute, Jena, 1881–88. Member of the Physio-Medical Society, Erlangen; Royal Academy of Science, Berlin; Academy of Sciences, Munich, Stockholm, Copenhagen; and many other scientific and learned societies. **Author of** *Text-Book of the History of Evolution of Man and of Vertebrates; The Elements of the Science of Evolution; Timely and Disputed Questions of Biology;* and numerous other works and memoirs on anatomy.]

From the time of Greek science until our own day, no other problem has interested the scientific investigator as much as that of animal development. Still after many centuries, difficulties remain that appear insurmountable to human powers. This is especially true of the secret problem of generation. In earlier centuries, the old anatomists with their incomplete methods of investigation could not win true knowledge, which, however, they sought to replace by hypotheses, which were generally without permanent value, and sprang from the earth like mushrooms. At the end of the seventeenth century more than 300 could be enumerated, and when the famous physiologist Haller brought together the work of several centuries, in his great handbook of physiology, he commenced the chapter on generation with the complaint, which was certainly justified at that time, "Ingratissimum opus, scribere de iis, quae multis a natura circumiectis tenebris velata, sensuum luci inaccessa hominum agitantur opinionibus."

The century of natural sciences, the nineteenth century, was the first to lay a scientific basis for the study of generation, as well as for that of so many branches of natural science. Since then such great advances have been made, that if Haller should, in our day, begin again to write the chapter on generation, he would certainly term it, in contrast to the year 1746, an "opus gratissimum."

For is it not a pleasant task to follow the way in which the torch of science has constantly more brightly illumined a realm, which for many centuries was looked upon as one of the most hidden; also how, on the successfully trodden way, the new discoveries have, with certainty and regularity, been crystallized around the already determined truth? Therefore, I may surely count upon a general interest when I give a comprehensive sketch of the position and problems of our present development in the realm of generation.

The theme corresponds also to the general programme of the Board of Managers of this Congress. It is their object to show, in the great series of addresses which lie before us, a proof of the inseparable connection of all branches of science. Our theme will show us, step by step, how botanists and zoölogists, students of the Protista, anatomists and physiologists, work hand in hand when they investigate the general basic truths of their various sciences in the realm of generation, as here, every step forward in one of these immediately assists each of the others. The goal of truth, for which we seek from various starting-points, is the great science of life, biology, to whose investigation the separate ways lead. In another connection still, we shall see how the development of biology is dependent, in more than one connection, upon the development of other sciences, especially of physics and chemistry, and thus forms an integral limb in the regular development of the great tree of knowledge. To give a convincing example of this natural connection, the most important discoveries which biology has made in the last hundred years were made possible, in great part, by the development of physics. Consider the advance in physical optics, and the technic connected therewith, which through Abbé's labors gave us the compound microscope, that wonderful instrument already brought to the highest perfection and destined to overcome, in the rapid course of conquest, the new world of the smaller micro-organisms. Embryological investigation, especially, was seen to take a great spring forward the moment physiologic knowledge showed that animals are built up of smaller individuals, the cells, and thus are nothing more than communities of innumerable, socially connected, elementary organisms. Embryology is indebted to the students of plant anatomy for the impulse toward this new study which is built upon the knowledge of the construction and origin of plants, based upon Schleiden's teaching. For, standing upon Schleiden's shoulders, Schwann has shown the dominion of the cell theory in the animal body.

At this time the study of generation received its first scientific basis. The beginning of individual life, the egg itself, is a cell, as Schwann had already conjectured. The spermatozoa also, which in the time of Johann Müller were frequently looked upon as parasitic organisms in the seminal fluid, comparable to infusoria, were soon explained by Kölliker as elementary parts of the animal, as they too arise from cells. Thus the organism reproduces new individuals of its own sort by loosing from their bonds single cells, as sexual products, which may begin an independent life in a new process of development. While until now the progress came from the botanical side, animal embryology, on the contrary, now began to have a fruitful influence on the study of generation in plants. The question which next pressed itself upon the embryologist was: Why must the egg, that the young being may develop from it, first experience the effect of the semen? Why must it, except in the rare cases of virgin generation, be fertilized? This matter still remained a problem which actively demanded a solution. Ordinarily the process was explained by saying that the egg, in order to begin development and to divide, needed an external stimulus, and that this stimulus to development was a chemical process arising either from the seminal fluid or from the spermatozoa.

Some investigators who endeavored to observe fertilization in suitable objects, believed that they were able to see under the microscope that some of the numerous spermatozoa which surrounded the ovum forced their way in, dissolved, and mixing with the yolk, acted as the fertilizing agent. For a time the question as to the penetration of the spermatozoa in the egg was the burning question of the day in science. What value was laid upon the observation of a spermatozoön inside the yolk-sac, may readily be seen from the fact that Barry, as well as Nelson, Keber, and Meissner, called together a congress of professors and doctors in order to show them the discovery, and to permit them to see the proof for themselves.

The state of the knowledge of generation up to the year 1875, Wundt has expressed as follows in his text-book of physiology: "The important condition for fertilization is, in all probability, the penetration of the spermatozoa into the egg contents, which may be shown in the various classes of vertebrates. After the spermatozoa have penetrated into the egg they rapidly lose their mobility and dissolve themselves in the yolk. We do not possess a theory, or even a plausible hypothesis, concerning the nature of the process, by which after their penetration into the yolk they provoke in this the process of development."

With the year 1875, a new stage begins in the study of generation. At that time I was fortunate enough during a long sojourn for study at the Bay of Villafranca to determine more accurately the process of fertilization, in an extraordinarily favorable object, the egg of the ordinary sea-urchin, *Toxopneustes lividus.*[1] As in the sea-urchin the

[1] My investigations on the first stages of development in the egg of the sea-urchin began Easter, 1875, in Ajaccio, where I studied especially the changes in the division of the egg. At that time, however, I did not succeed in observing the process of fertilization, although my attention was directed toward it. I first succeeded when I went from Corsica to Villafranca, with my brother (who was making a study of *Radiolaria*) and there continued my investigations for some time. When, therefore, Bölsche, in the first volume of his encyclopædia *Men of Our Time*, p. 228, writes: "Oscar Hertwig made in Ajaccio the discovery of the act of fertilization in the sea-urchin which will form for a long time a turning-point in the history of our knowledge of the sexual act of generation, thus of one of the deepest mysteries of all nature," the name of the place Ajaccio should be replaced by Villafranca.

sexes are separate, and as the eggs which almost the whole year through may be found in the mature condition are small and transparent, it is here an easy task to observe the artificial fertilization on the object-glass and under the microscope. The complete transparency of the egg permits, even with extreme magnification, the most minute processes to be observed during life. That which has already been discovered can be controlled and more accurately determined in many details in preserved material.

Thus the important points of the process of fertilization could be explained and later positively determined by me and the numerous investigators who have since then occupied themselves with the *Echinodermata* (Diagram I).

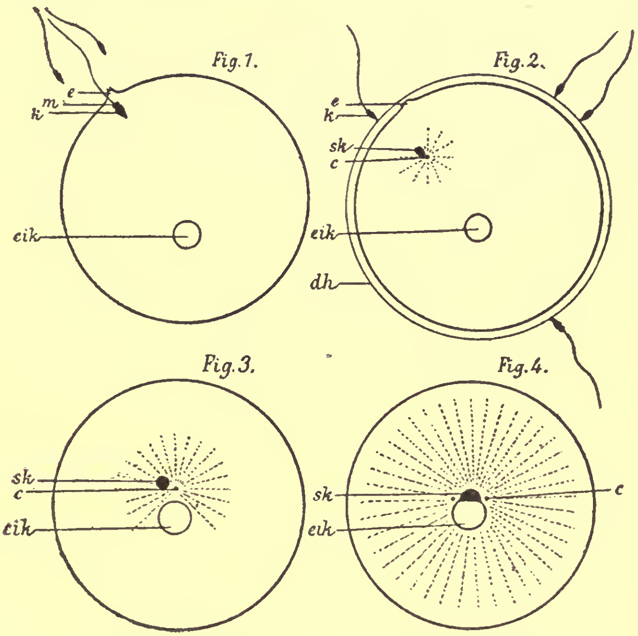

DIAGRAM I. The fertilization process in the ovum of *Toxopneustes lividus*.

FIG. 1. The mature egg at the moment of fertilization. Of the numerous spermatozoa one has already penetrated the egg at a point which is determined by the "reception eminence." In the spermatozoön the head (*k*), the middle piece (*m*), and the terminal filament may be distinguished. The egg-nucleus (*eik*).

FIG. 2. The egg a few minutes later has excreted the yolk-sac (*Membrana vitellina*). The head and the middle piece have separated from the terminal filament, which has disappeared, and have changed into the male pro-nucleus (*sk*) and the centrosome (*c*). The latter is surrounded by protoplasmic rays. The distance between the sperm-nucleus and the egg-nucleus has lessened.

FIG. 3. A few minutes later. The egg- and sperm-nuclei have approached one another in the centre of the ovum. The originally simple centrosome has divided in two. The protoplasmic rays around the two nuclei have become larger.

FIG. 4. The egg- and sperm-nuclei lie against one another and have become flattened at the place of contact. The centrosomes are arranged on opposite sides of the nuclei. The protoplasmic rays have spread themselves out over the entire yolk.

After the mixing of the sexual products, numerous spermatozoa approach the egg-cell by a swinging motion of their tails, but only one penetrates, if the egg is normal and capable of life (Fig. 1, *k* and *m*). The point of penetration is known to be a small conical process, the reception eminence (*Empfängnis Hügel*), which extends from the egg-surface toward the closest spermatozoön. To others, entrance is immediately made impossible by the fact that the egg at once excretes a fine but impenetrable skin, the *membrana vitellina*, largely as a protection against this.[1]

The internal fertilization process immediately follows the external. Of the three parts which, as is well known, may be distinguished in the spermatozoön, the head, the middle piece, and the contractile terminal filament, the last is thrown off and has no more importance in the process. The head, on the contrary, which was formed from the nucleus of the spermatozoön-forming cell, and which contains the chromatin (Fig. 1, *k*, and Fig. 2, *sk*), begins to change into a small round vesicle which I have called the seed or sperm-nucleus, and which by the absorption of juice from the protoplasm begins slowly to increase in size (Figs. 3 and 4, *sk*). The middle piece (Fig. 1, *m*) contains a tiny cell-organ, the much-studied centrosome (Fig. 2, *c*), which in spite of its extreme minuteness plays a striking and important rôle in the division of the nucleus. It moves in front of the sperm-nucleus, and its position in the living cell is easily recognizable, because in its neighborhood, evidently as a result of a stimulus proceeding from it, the protoplasm arranges itself in radial bands in a figure like iron-filings around the pole of a magnet.

Interesting phenomena begin now, in rapid succession, to fix the eye of the observer. The original nucleus of the egg and the newly introduced sperm-nucleus draw mutually together and move with increasing rapidity through the yolk toward one another (Figs. 2, 3, and 4). The sperm-nucleus (*sk*) which is constantly preceded by the radiance with the centrosome (*c*) included therein, changes its place more quickly than the egg-nucleus. Soon the two meet in the middle of the egg (Fig. 3), where they are inclosed by a common radiance which has now extended over the entire yolk. They lie against one another, becoming flattened on the contact surfaces, and then lose their separation from one another with the formation of a common nuclear sac. Egg- and sperm-nucleus are thus united to form a common egg-nucleus in which the chromatin of the male and female sexual cells is contained. At this point the internal process of fertilization may be looked upon as concluded.

Two or more nuclei in the egg-cell were already described several

[1] The formation of the *Empfängnis Hügel* was first observed by Fol, when, in connection with my experiments, he made a very thorough study of the fertilization process in *Echinodermata* (*Recherches sur la fécondation et le commencement de l'hénogénie*, Genf, 1879).

times before 1875 in different objects (mollusks, nematodes) by Warneck (*Ueber die Bildung und Entwickelung des Embryos bei Gastropoden, Bull. de la soc. des. Natur. de Moscou,* vol. XXIII), Bütschli (*Studien über die ersten Entwicklungsvorgänge der Eizelle,* 1876), and Auerbach (*Organologische Studien,* vol. II, 1874), and their coalescence with one another was observed. It, however, occurred to no one to see in this coalescence of egg- and sperm-nuclei the process of fertilization. The nuclei were looked upon as new formations (vacuoles) in the egg whose nucleus had been lost. Bütschli believed that the germinal vesicle was completely thrown off. Auerbach thought it was dissolved by karyolysis. Thus it was taught that when seminal bodies penetrated into the egg-cell, they were destroyed by complete solution.

Born is therefore wrong when he states in an article which appeared in 1898 (*Anatom. Anzeiger,* vol. 14, no. 9), "Auerbach has given the modern study of fertilization its lasting basis. It should never be forgotten that this service belongs to Auerbach alone."

Auerbach was far away from the correct interpretation of the phenomena. He knew only that through the coalescence of two nuclei which arose as vacuoles in the yolk at opposite ends of the egg, material differences, individual mistakes in composition, between the two halves, were adjusted. According to his conception, "The necessity for the whole complex of phenomena is caused by the special peculiarity of the fertilized Nematode eggs, namely, by their elongated shape and by the peculiar condition during the act of fertilization by which the eggs forcing themselves through a narrow canal offer at first only their anterior polar region to the zoösperms."

Otherwise, Auerbach has expressed himself very correctly as to the relation between his and my investigations in speaking of my work (*Jenaer Literatur Zeitung,* dritter Jahrgang, 1876, no. 101, p. 107). After a short reference to the contents, he remarks: "These observations confirm, as the author explains, as regards the conjugation of two nuclei of independent origin in the egg, those of the writer, but vary from these in that the author ascribes to the two nuclei not merely, as the present writer, a slight qualitative difference caused by fertilization, and does not look upon them merely as new formations, but rather sees in one the morphological remainder of the egg-nucleus, in the other that of the sperm-cell. It is evident that if, in the further development of the subject, the results won by the author should be confirmed, a new light will be thrown upon the fertilization process, the aim of which would be accordingly a conjugation of the nuclei of a male and female sexual cell." Hensen was among the first to value correctly the importance of the theory of fertilization proposed by me. In his article "The Physiology of Generation," in Hermann's *Handbuch der Physiologie,* vol. VI, part 2, p. 126, he remarks: "This conception of fertilization must be looked upon as a fortunate one. It deepens our knowledge of the process of fertilization because it adds to the previously considered chemical and physical elements the morphological element which is so important in the phenomena of life and inheritance by showing that the essential substance has a definite form. Also the new experiences with regard to the important rôle which the nucleus plays in cell-division, as well as for the study of fertilization, come into play, and at the same time the formation of the polar bodies as a preparatory stage for the conjugation of the nuclei is explained in a far better way than was previously possible."

On the basis of these observations fertilization may be looked upon as union between two different cells which arise from a male and a female individual. The essential in this process is evidently the union or, to use the expression of Weismann, the amphimixis of the egg and sperm-nuclei. That this is a general law of biologic nature is now doubted by none. For fertilization is the same process in all classes of animals as in the *Echinodermata*. Many of these, such as *Cœlenterata* and *Vermes*, as *Tunicata* and *Mollusca*, as *Crustacea* and *Insecta*, have been investigated by various scientists. The numerous *Vertebrata*, in which the process has been followed, *Mammalia*, *Reptilia*, and *Amphibia*, *Cyclostomen* and *Amphioxus*, all show the same process.

The discovery of the fertilization process in animals has immediately brought about similar discoveries in the plant kingdom. The fertilization of *Phœnerogamia*, previously studied without result by many investigators, was now quickly explained by Strasburger. Our knowledge in this and other points was completed by Guignard, Nawashin, and others. We now know that the pollen grain, which is analogous to the spermatozoön of animals, carries into the egg-cell of the ovary a sperm-nucleus which combines with the egg-nucleus. The correspondence is even greater in the *Cryptogamia*, as here externally the vegetable spermatozoid is very similar to the animal spermatozoön, and fertilization proceeds in a similar way. Even among the lowest organisms, *Infusoria*, *Rhizopoda*, *Flagellata*, *Algae*, and *Fungi*, the process of fertilization is seen to be the same.

By this natural law of sexual generation, which is now so surely founded and based upon a complete series of observations, the old discussion which once played so great a rôle in the history of the sciences and engaged for a long time the naturalists and philosophers, the strife between the Ovists and the Animalculists, has been decided.

From the sixteenth to the eighteenth century the dogma of preformation ruled : the doctrine that the embryo of a being was built up of the same organs and parts as the parent, and thus was nothing less than an extraordinarily minute reproduction of it. Most scientists (Swammerdam,Harvey, Spallazani, Bonnet, Haller) looked upon the egg as the preformed embryo, as may be seen from the well-known saying, "omne vivum ex ovo." But when Leeuwenhoek, during his microscopic discoveries, found the spermatozoa, the thought occurred to him that the worm-like bodies in the semen which moved independently, and thereby showed a certain resemblance to the lowest organisms, should be more properly considered as the miniature beings. He, therefore, proposed the hypothesis that the spermatozoa penetrated into the egg during fertilization in order that the latter might serve them as a suitable nourishment for their future growth. No less a person than Leibnitz accepted this hypothesis.

Strangely enough, in both hypotheses, which appear to be excluded together with the dogma of preformation, a seed of truth seems to be hidden. For, as is easily seen from our present standpoint, both egg and sperm take an equal part in the formation of the new being. Both are cells, one of which represents the properties of the female, the other the properties of the male progenitors. Both unite to produce a mixed product, which has inherited the peculiarities of both parents.

Here we see again how the development of scientific views in the realm of embryology is dependent upon the contemporary development of all science. We can appreciate the fact that the old scientists could not understand the process of generation, because at that time the lack of microscopic assistance hid from them the conception of the elementary construction of the organisms.

The thought of the union of two organisms into a new unit could not occur to the adherents of the preformation theory, for if embryos are already miniature beings composed of many organs, how could it be possible that they should unite in pairs to form a single individual, and at the same time their organs and tissues flow together into one?

For us who know that the germs are merely cells separated from their parents, thus similar to simple elementary organisms, the conception of an amphimixis has no such difficulty, and for us it is now a determined fact. We can follow under the microscope the union of a male and a female cell and even the union of their component parts, especially their nuclei and the substances contained therein. With the knowledge of amphimixis the phenomenon that children may resemble both their parents, a fact for which scientists until the nineteenth century could give no logical explanation, is brought within our understanding. They resemble both, because they are formed from a union of the substance of the father and mother; in other words, from a paternal and a maternal element.

At this point the problem of generation and fertilization passes over into the most difficult of all problems, the problem of inheritance. However, before we approach this more closely, it will be well to make ourselves familiar with the series of phenomena which stand in the closest relation to the problems of generation and inheritance and also belong to the most important discoveries of modern biology. Here also the discoveries for which we must thank, in the first place, zoölogists and embryologists, have reacted favorably upon the investigations of botanists.

The older zoölogists, Fritz Müller, Loven, and others, had already noticed that from the egg-cells of the most distant classes of animals two minute spheres of protoplasm were thrown off, a short time before or during fertilization (Diagram III, Figs. 3, 4, 5, pz^1, pz^2p). These were called the polar bodies, because at the place of their extrusion from the ovum the first plane of segmentation began. Their importance remained an enigma. Many scientists believed that they constituted an excretion by the extrusion of which the egg purified itself of useless substances, before the beginning of its further development. Then Bütschli observed that the nucleus of the unfertilized egg is concerned in the formation of the polar bodies, that it projects from the surface of the yolk in the form of a nuclear spindle, which, as he believed, is then extruded in the form of the polar bodies. This was a great advance, but combined with an error with regard to the entire meaning of the process which soon after was rightly determined by Giard and myself. For more accurate investigation showed us that the polar bodies were not formed by extrusion, but by two true divisions which followed immediately upon one another, and that in the second division half of the spindle and of the chromosomes remained behind in the egg, and here became the nucleus of the mature egg. The process only differed from an ordinary cell-division in that the parts were so unequal in size. The polar bodies should, therefore, better be denoted polar cells.

For what reason and to what end, we may ask, are these two insignificant polar cells formed with such great regularity in the entire animal kingdom? On this also light was soon thrown by the accurate study of an extremely favorable object for investigation, the egg of the horse roundworm, *Ascaris megalocephala*, which has been as productive of results in the study of the process of fertilization as the egg of the *Echinodermata*. Its invaluable advantage consists in the fact that it gives us a deeper insight into the relation of that substance which plays the most important rôle in the division of the nucleus, namely, the chromatin.

Of the chromatin we know by investigations which are among the most brilliant of the histological advances of the last decennium (see Diagram II, showing nuclear and cell division) that the chromatin at the beginning of the nuclear division is changed into a long convoluted chromatin thread, and that this in the second phase (Fig. 2) breaks up by cross-segmentation into a very definite number of segments or chromosomes (*ch*) which arrange themselves in the middle of the nuclear spindle (Fig. 3, *sp*) to a symmetrical figure,

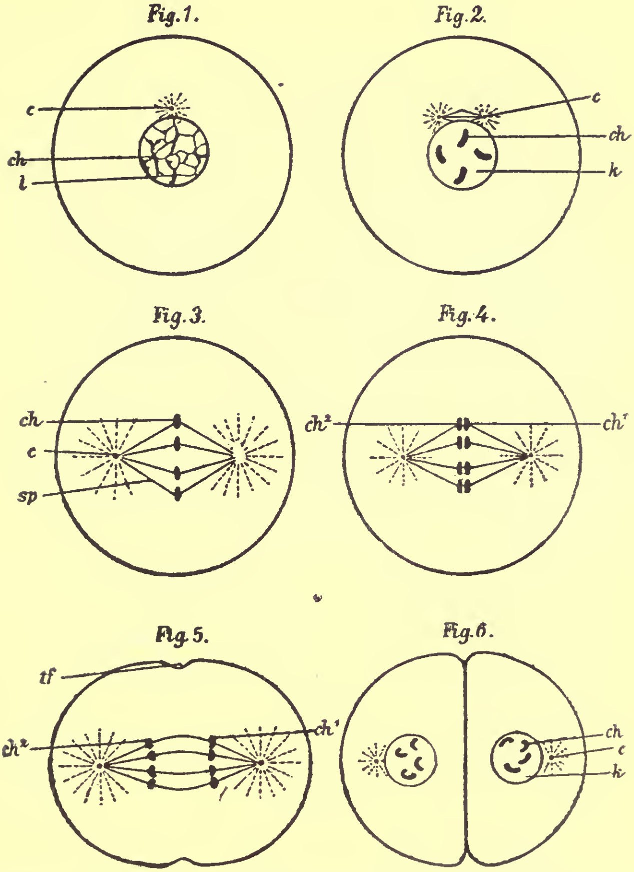

Diagram II. Six stages of cell-division and nuclear division (*Karyokinesis*).

Fig. 1. The first stage. Cell in the resting spherical form, showing a nucleus and one centrosome (*c*). The nucleus shows a network of linine with threads and granules of chromatin (*ch*).

Fig. 2. Second stage. During the preparation for division (pro phase) the chromatin has drawn together into a thread which has immediately broken up into four pieces (chromosomes). The centrosome (*c*) of Fig. 1 has divided, and between the two parts a spindle has arisen.

Fig. 3. Third stage. The spherical nucleus has dissolved. The two centrosomes of Fig. 2 are more widely separated and the spindle between them has become much larger. The four chromosomes (*ch* of Fig. 2) have arranged themselves symmetrically in the middle of the spindle to form the mother star.

Fig. 4. Fourth stage. The four chromosomes of the spindle have split longitudinally each into two daughter chromosomes (*ch* 1 and *ch* 2).

Fig. 5. Fifth stage. The daughter chromosomes which arose by longitudinal splitting have separated further and further from one another toward the opposite ends of the lengthening spindle (formation of two daughter stars). The cell begins to segment in the middle.

Fig. 6. Sixth stage. The segmentation has become complete, and the mother cell is thereby divided in half. In each daughter cell a spherical daughter nucleus, which contains the chromatic substance of four daughter chromosomes (*ch*), has arisen from half of the spindle. By each daughter nucleus (*k*) lies a centrosome (*c*).

the mother star. Each chromosome then begins to split longitudinally into two identical parts, the two daughter chromosomes (Figs. 3, 4, 5, *ch*). We are justified in seeing in this the true task of the complicated nuclear division, as the two halves now move away from one another toward the opposite ends of the nuclear spindle (Fig. 5, ch^1 and ch^2) and form the two daughter stars, which after the division of the cell in two parts form in each the basis of a daughter nucleus. These promptly return to the spherical form.

Extended comparative observations in the most widely separated classes of animals have demonstrated a definite numerical law in the chromosomes. It states: In all cells of an animal or plant species the same number of chromosomes always arise during a division of the nucleus. In one species four, in another twelve or sixteen or twenty-four, etc. The number of chromosomes is four only in one variety of *Ascaris*. For this reason, and because the few chromosomes are at the same time of very considerable size, the eggs of the horse roundworm are of great advantage for studies in the question which now concerns us.

These remarks with regard to the phenomena of nuclear division must first be made, in order to understand the progress which has been brought about by the study of *Ascaris* eggs in the remarkable investigations of van Beneden, which immediately followed the excellent work of Boveri.

Two fundamental facts were discovered concerning the behavior of the chromatin in the *Ascaris* egg (Diagram III). One of these facts concerns the process of fertilization. Egg- and sperm-nuclei (Fig. 5, *eik* and *sk*) remain, in the egg of *Ascaris*, separated from one another for several days, and prepare themselves separately for the formation of the first karyokinetic spindle. From the chromatin network, chromosomes arise in the way described above, two in the egg-nucleus (Fig. 5, *wch*), two in the sperm-nucleus (*mch*). We can thus easily follow their fortune in the further stages of division, and determine that of the four chromosomes of the nuclear spindle, two arise from the egg-nucleus, two from the sperm-nucleus. When the chromosomes split longitudinally, in the stage of the mother star, we see their products, the daughter chromosomes, separate from each other, in the way described above (Fig. 7, *wch* and *mch*), to form the daughter stars, and finally enter into the formation of the daughter nuclei of the two new cells. In this case incontrovertible proof has been brought that in the first division of the fertilized egg an equal amount of chromatin from the egg-nucleus and the sperm-nucleus is brought to each of the daughter nuclei.

This process apparently repeats itself in every later division, so that finally the nucleus of every tissue cell is composed of equal amounts of chromatin of maternal and paternal origin, which has

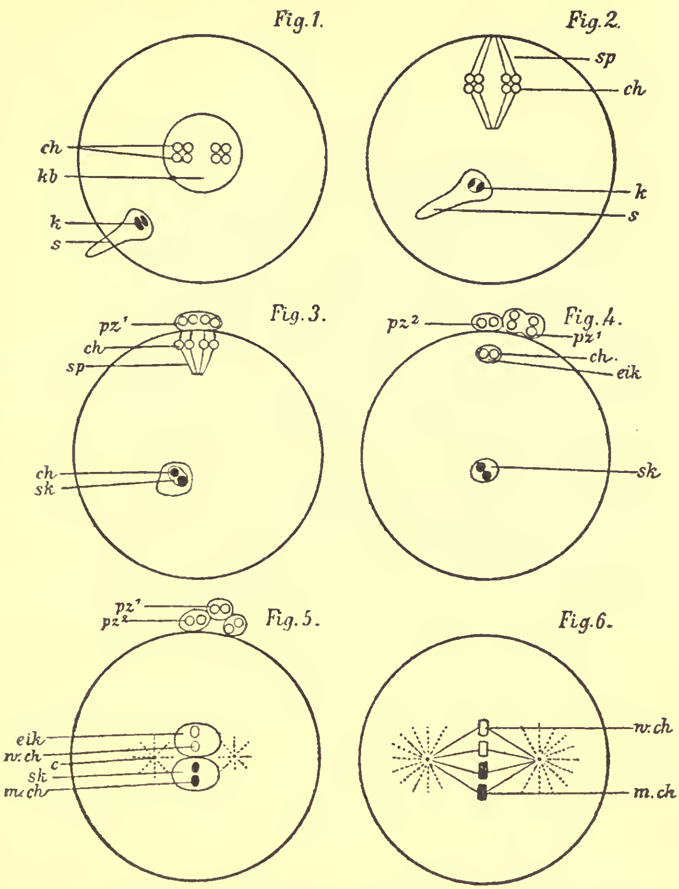

DIAGRAM III. The process of fertilization, the formation of polar cells and the first division of an egg of *Ascaris megalocephala bivalens.*

FIG. 1. The egg at the moment of fertilization. It shows still a spherical nucleus (*kb*) in which the chromatic substance is arranged in two groups of four (tetrads, *ch*). The spermatozoön, shaped like a tailed sphere, has pressed halfway into the egg. Its nucleus (*k*) is composed of two chromosomes.

FIG. 2. From the spherical nucleus a spindle with two tetrads has arisen (*ch*). The spermatozoön (*s*) has pressed into the middle of the egg.

FIG. 3. At the animal pole of the egg, where the spindle lay in Fig. 2, the first polar cell (*pzl*) has been formed by budding. It receives from each tetrad of the spindle two chromosomes connected in pairs (a dyad), while the other two chromosome pairs (*ch*) remain behind in the egg with the half spindle (*sp*). The spermatozoön (*sk*) begins to dissolve, except the nucleus, which begins to become spherical.

FIG. 4. In the same way as the first the second polar cell is formed by budding (pz^2). From each of the pairs of chromosomes (Fig. 3, *ch*) of the previous stage, a chromosome comes to live in the second polar cell, while the other remains behind in the egg and forms the egg-nucleus (*eik*), which then contains two chromosomes, as does the spermatazoön (*sk*).

FIG. 5. Egg- and sperm-nucleus approach each other until they touch, but do not unite. In order to distinguish their chromosomes those of the egg-nucleus are drawn as a white circle (*wch*), those of the sperm-nucleus as a black circle (*mch*), as was done in the previous Figs. 1 to 4.

FIG. 6. Egg- and sperm-nuclei have together formed a spindle of whose four chromosomes half (*wch*) arise from the egg-nucleus, the other half (*mch*) from the sperm-nucleus. The polar cells, as in Figs. 7 and 8, have been omitted.

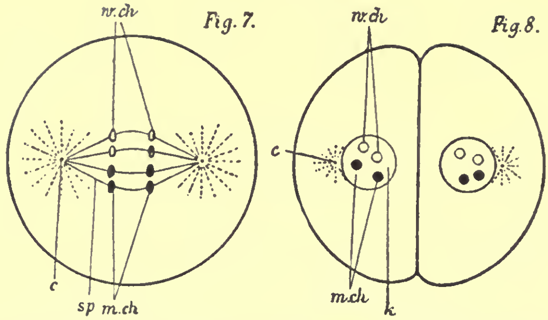

FIG. 7. The female and male chromosomes of Fig. 6 have divided longitudinally and separated from each other in two groups of daughter chromosomes: (*sp*) spindle; (*c*) centrosome.
FIG. 8. The two halves of the egg contain daughter nuclei, half of whose chromosomes arise from the egg-nucleus, half from the sperm-nucleus.

been constantly increasing by growth. Of course the equal division cannot be determined later by direct observation, as is the case in the first division, but after what we know of the nature of nuclear division this view may be considered in the highest degree probable.

Still more important is the second fact determined on the *Ascaris* egg. The chromosomes of the egg- and sperm-nuclei are an exception to the above-mentioned numerical law. Whereas in *Ascaris megalocephala bivalens* four chromosomes always arise from the resting nucleus, only half as many, that is, two, occur in the egg- and in the sperm-nuclei (Figs. 4, 5, *eik* and *sk*). How is this exception from the numerical law to be explained? How is it brought about? A very accurate study of the method of origin of the polar cells, as is possible in *Ascaris*, gives a satisfactory explanation.

Some time before the origin of the polar cells remarkable changes occur in the contents of the nucleus which justify the great consideration which they have received, and which have been the object of extended investigation. In this variety of *Ascaris* four long threads arise from the chromatin network and split longitudinally into double threads before the height of karyokinesis, the usual time of splitting. These threads immediately place themselves across each other, and thus produce, while gradually becoming shorter, a tetrad of chromosomes, a stage which has been shown in the development of many species of animals. When now the nucleus dissolves and the first polar spindle is formed from its contents, the eight chromosomes arrange themselves in the middle, in two tetrad groups. Later each tetrad group, of the first polar spindle, separates into two groups of chromosomes, connected in pairs (Fig. 3), or in other words, each tetrad divides in two dyads, of which one passes into the first polar cell (*pzl*), the other passes into the egg.

And now there occurs a second striking variation from the usual process of nuclear and cell-division. While otherwise, after division, the nuclear substance always passes for a time into the spherical resting state, here it immediately prepares itself for a second division, which leads to the cutting-off of a second polar cell. The half of the first polar spindle remaining in the egg (Fig. 3, *sp*) immediately enlarges itself into a second complete spindle, in whose middle the two dyads lie. These immediately separate into their individual elements, of which two are taken up into the second polar cell (Fig. 4, pz^2), and two remain in the egg, and here form the basis of the egg-nucleus. Thus of the entire chromatin mass of the egg-nucleus which was divided into eight chromosomes, the mature egg only contains the fourth part, that is, from each of the two tetrads only one single chromosome (Fig. 4, *eik*, *ch*). Instead of once, as in usual cell-division, the chromatin has been divided twice by two polar divisions; in other words, it has been quartered. Therefore, the egg-nucleus only contains half as much chromatin as the nucleus of an ordinary tissue-cell or an embryonal cell. Immediately after each division, it is, to a certain extent, only half a nucleus, and as such is an exception to the numerical law of chromosomes. Weismann has called the whole process, by which is effected the reduction of the nuclear mass and the number of chromosomes to half, a "reduction division."

As the sperm-nucleus in *Ascaris* only possesses half the number of chromosomes of a normal nucleus, the conclusion may be drawn, that in it also a reduction must have occurred, as occurs in the egg by the formation of the polar cells. By such consideration, I was led to seek for a corresponding process in the formation of sperm, which premise showed itself as correct.[1]

As an accurate comparison of the egg- and sperm-formation in *Ascaris* shows, there exists in the two a complete parallel, which may be followed into the smallest detail. The unripe egg with a spherical nucleus, the egg mother cell or ovocyte (Diagram III, Fig. 1), corresponds to the sperm mother cell or spermatocyte (Diagram IV, Fig. 1), as each undergoes a reduction by the formation of polar cells. Also the chromatin arranges itself in the nucleus in this extremely characteristic way which is observed nowhere except in sexual cells in two groups of four each (Diagram IV, Fig. 1 *ch*.)

[1] Even before my investigation Platner determined by a study of the process of sperm-formation in *Lepidoptera* and *Pulmonata* a reduction process in the sperm-nuclei, although in a less striking and less comparative way. He drew the conclusion "the spermatocytes correspond to the ova. In both cases a reduction of the chromatic substance to a quarter of its original quantity occurs, while a second division follows immediately on the first without a period of rest between." (Platner, *On the Meaning of the Polar Bodies, Biologisches Centralblatt*, vol. VIII, p. 193, 1889, and *Contributions to the Knowledge of the Cells and their Division, Arch. für mikrosk. Anat.*, vol. XXXIII, 1889.)

Then the sperm mother cell is split up by two divisions, which follow upon one another without a resting stage being interposed, first into two daughter cells (Fig. IV), and immediately by a second division which causes the actual reduction into four granddaughter cells of equal size. By these processes, each of the two tetrad groups (Fig. 2, *ch*, and Fig. 3) divide into two pairs of chromosomes, which are shared by the two daughter cells (Fig. 4). Then each pair of chromosomes (Fig. 5, *ch*) falls again into its individual elements, which are taken up by the granddaughter cells (Fig. 7). These, therefore, contain, as does the mature egg and the polar cells, only a single chromosome from each tetrad group, altogether only two (Figs. 7, 8). Their nuclei are, therefore, reduced to half-nuclei.

Many will have asked, what aim this noteworthy reduction of the chromatin, which constitutes the important process of egg- and sperm-ripening, may have. The explanation is easily seen if we consider, in connection with the chromatin reduction, the succeeding fertilization, and consider that by this a second nucleus is brought into the egg, which combines with the egg-nucleus and thus doubles its chromatin mass. Thus from two half-nuclei a complete nucleus is again formed, from which then arise all the nuclear generations of the new being. Thus ripening and fertilization of the egg stand to one another in a supplemental relation. That fertilization is needed to replace the chromatin reduction may be proved by a consideration.

As the numerical law of the chromosomes has taught us, chromatin is a substance which shows a tendency to be constant in a given species, not only in relation to its mass, but also in regard to the number of chromosomes in which it splits during karyokinesis. Thus it is a substance which after cell-division increases to the double and is then halved by division, etc. If we now consider that the process of reduction did not occur, then by fertilization two complete nuclei would be united, and the result would be a doubling of the chromatin, in relation to the normal. By every new sexual generation the same process would be repeated, and thus in the course of generations a summation of nuclear substance would be brought about, which in a short time would lead to such a lack of relation between it and the protoplasm, that the contents of a cell would no longer have room for it.

Led by similar considerations we may say: By the reduction which precedes fertilization the summation of the nuclear mass and the number of chromosomes to the double and multiple which is normal for the species under consideration, is hindered in the simplest way possible.

Thus, the phenomenon of reduction is a general biologic law of the greatest value. What has been observed in one species of animal has gradually been confirmed in numberless other cases, in vertebrates and invertebrates. And time and again that which we have already seen has been repeated. These discoveries of the embryologists placed new problems before the botanist, which he immediately seized and solved. In the sharper position of the question which was now possible, phenomena were gradually observed in the *Phænerogamia* and *Cryptogamia,* which, although no tso easily explained as in the animal kingdom, showed that, in the development of the vegetable sexual products, a reduction process by nuclear divisions following close upon one another, also occurred. Even in *Infusoria* and different sorts of lower unicellular organisms, corresponding processes have been observed.

We have reached in the realm of the study of generation a position which has been attained to the same degree in the study of very few of the other complicated phenomena of life. We can unite many facts in a few general laws which possess value for the entire organized world and for which we can use the expression "law" with the same justification and in the same sense as physicists and chemists in their determinations of law-abiding phenomena of lifeless nature. In a few decennaries discoveries have been made, which, supplementing each other, have been connected with each other, and have deepened in an unsuspected way our knowledge of generation.

And as the middle point of these discoveries there stands a well-characterized substance, which is contained in a small amount in the nucleus of every cell, and whose striking changes during cell-division have drawn upon it the attention of biologists, the chromatin. That this wonderful substance must have a great importance in the life of the cell is hardly to be doubted after the foregoing experiences. Let us attempt to penetrate somewhat deeper into its importance. We are hereby brought back to the important problem of inheritance upon which I already touched in connection with the demonstration of fertilization, but had retained for later mention. If the egg- and sperm-cell conveys to the new being the properties of the father and mother, how does it come about, we may ask, that these share in the process to such an unequal degree, as the egg gives to the new being one hundred or one thousand times more substance than the insignificant spermatozoön? Naegeli, in his book *Concerning the Mechano-Physiologic Theory of Generation*, which is very rich in ideas, has attempted to answer the question by theoretic discussion, by the view that the sexual cells consist of different substances, which possess a different value for the inheritance of parental characteristics. The important sort he designates idioplasm.

Idioplasm is a purely hypothetic conception, for Naegeli himself has not stated what substance in the cell is actually the idioplasm. A real basis must therefore first be won by empiric investigation. This occurred contemporaneously and independently by Strasburger and myself; Weismann, Kölliker, and others soon followed.[1]

Proceeding from the facts of karyokinesis, of fertilization and maturation, I concluded that the substance of the nucleus, and here, especially the chromatin, corresponded to the idioplasm of Naegeli. Three important considerations appeared to me to point in this direction.

First: The chromatin is the only substance known to us which occurs in exactly equal amount in the sperm- and egg-cells. As a proof I will recall briefly the already mentioned brilliant discovery of van Beneden, according to which the egg- and sperm-nuclei of *Ascaris megalocephala bivalens* contain the same number of chromosomes, that is, two, which are of equal size.

Second: the fact that the chromatin is the only substance which passes over in equal quantity from the mother cell to the daughter cell, after it has doubled its volume by nourishment and growth. The complicated process of karyokinesis evidently serves only for this purpose. The arrangement of the chromatin particles in threads, the division of the chromosomes longitudinally, the distribution of their split halves toward the poles of the spindle, and the equal distribution in the daughter cells.

Thus, this substance, in which rests the peculiarity of the organism, is carried down from one cell generation to the next as a valuable inheritance, and thereby is the principle by which every cell of the organism is "idioplasmatically enabled," as Naegeli expresses it, to become the germ of a new individual. Here also numerous phenomena of generation and regeneration find their explanation. For in many plants and lower animals we see that actually almost every small cell complex separated from the rest of the organism is able to reproduce the whole. From the root-cells of a plant, buds may form, to reproduce the aërial part, and from the stem-root, cells may develop, as is seen in slips. This is because, in cells, which during the course of development have adapted themselves for a certain function, the deposits contained in their inherited mass are still slumbering, and may be newly awakened and forced into a definite development.

Thirdly and finally, we may base our opinion upon the chromatin reduction. I might denote this as a proof of the justification of the theory. Without having known of the finer processes which occur during the formation of the polar cells, Naegeli had already

[1] I have given the different historical and critical opinions, in regard to the theory of fertilization and inheritance, in my article *Comparison of Egg and Sperm Formation in Nematoda, Arch. für mikrosk. Anat.*, vol. XXXVI, pp. 77–127, 1890, and in *Zeit. und Streitfragen der Biologie*, vol. I, p. 16, 1894.

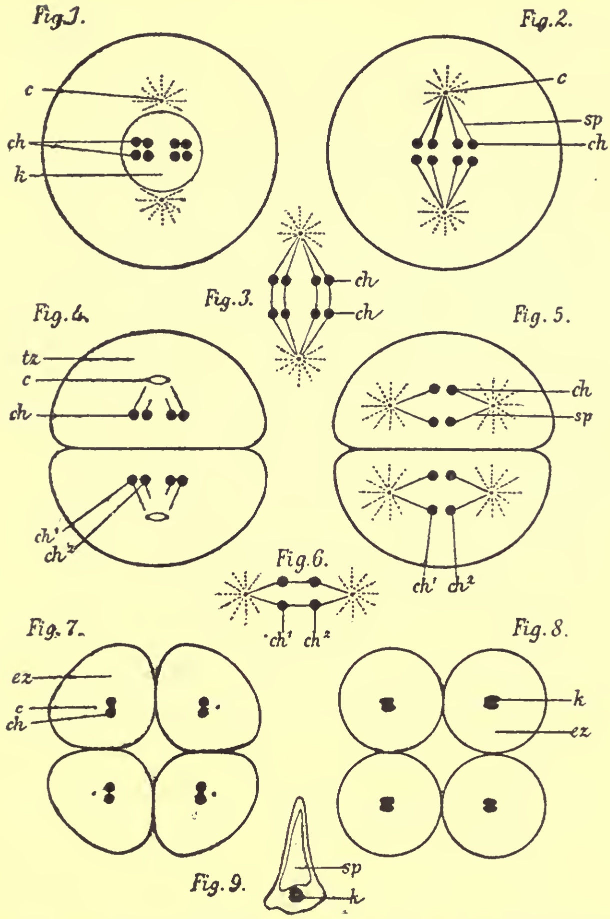

DIAGRAM IV. Spermatogenesis, or development of the seminal bodies from the seminal mother cells (spermatocytes) in *Ascaris megalocephala bivalens.*

FIG. 1. Seminal mother cell with a nucleus (*k*) in which two tetrads (*ch*) have formed. Centrosome (*c*) with rays.

FIG. 2. Seminal mother cell from the nucleus of which a spindle (*sp*) with two tetrads has developed. Centrosome (*c*).

FIG. 3. Spindle in which each tetrad has divided into paired chromosomes (dyads).

FIG. 4. The seminal mother cell is divided into daughter cells (*tz*) each of which incloses a spindle with two pairs of chromosomes (dyads) (*ch*). The centrosome (*c*) has divided into two daughter centrosomes between which a small new spindle is formed.

FIG. 5. The new spindle (*sp*) in each daughter cell has enlarged and included the two pairs of chromosomes (ch^1 and ch^2).

FIG. 6. In each spindle the pairs of chromosomes have separated from one another and approached the poles of the spindle.

FIG. 7. The two seminal daughter cells have divided into four granddaughter cells (*ez*), each of which includes only two chromosomes (one element of the tetrad of Fig. 1) and one centrosome.

FIG. 8. The two chromosomes of the granddaughter cells (*ez*) have flattened against each other eventually to form one small, compact, spherical nucleus (*k*).

FIG. 9. Each granddaughter cell changes into a seminal body (*sp*) conical in shape. Nucleus (*k*).

shown the necessity of a reduction process from purely theoretic considerations. He said: "If, in every propagation by fertilization, the volume of the idioplasm, however constituted, doubles itself, the idioplasm body would be so much increased, after several generations, that it could no longer find room in a spermatozoön. It is thus absolutely necessary that indigenous propagation the union of the parental idioplasm bodies occur without causing, by the united mass, a corresponding increasing growth of this material."

The process suspected by Naegeli was soon after discovered in the development of the polar cells, which, however, were first explained in another way by their discoverer himself, Ed. van Beneden, and were first recognized by Weismann as the process by which a summation of the parental mass as a result of fertilization was prevented. Weismann agrees with Naegeli that reduction was so certainly required by theoretic considerations that the process by which this occurred must be found if it were not contained in already known facts. I, however, doubt as little as does Weismann that the reduction of the idioplasm, which is theoretically demanded, occurs by the formation of polar cells.

When one fact thus agrees with another, which is very rare in this way in biologic processes, we may certainly say, in spite of the objections raised by several investigators, that the idioplasm of Naegeli is found in the chromatin of the cell-nucleus, and that this hypothesis is adapted in a high degree to serve as a starting-point and leading star.

How many questions whose solutions in part we are already beginning to determine, which in part wait upon the future, force themselves upon the investigator!

Does an actual penetration of the two idioplasms occur during the union of the egg- and sperm-nuclei, or do they remain alongside of one another, temporarily or permanently? and in corresponding way, how does the reduction process act? To how many questions, again, the origin of female and male sex and the generation of bastards gives rise! May we find a morphological basis by the study of the sexual production of bastards for the law of Mendel, which has been confirmed in great part by recent investigations of Tschermak, Correnz, and De Vries on bastards?

And what a perspective the following consideration opens! If the chromatin is the substance by which the peculiarity of each organism is determined, it must be of somewhat different composition in each of the numberless organized species. In the insignificant mass of an egg-nucleus, or a sperm-nucleus in the head of a spermatozoön, only visible under the microscope, the numberless peculiarities by which one species is separated from another are compressed in their elementary forms. Will human intelligence ever succeed in penetrating into this world of the smallest organic differences, which are now invisible to us? Will, in the future, the means of investigation of the biologists, perhaps the discovery of a more powerful microscope and the mastery of the same, increase the circle of vision of our successors as much as was done by the discovery and mastery of the compound microscope?

Or, will the chemist succeed in so increasing his knowledge of the nature of proteid bodies that we may expect valuable conclusions in regard to the nature and difference of idioplasm, that is, the chromatin substance, from this direction? Who will dare to determine where, and how far away, a limit may be set to the possibility of human knowledge?

Far, far away lies in any case the goal, shimmering before us in the distance. For its attainment the individual branches of natural science, from to-day on, must have united themselves, by extension of their borders, to a great united science of nature, as the leading spirits are now trying to consummate. For the investigator who will busy himself with this deepest problem of life must unite in one person biologist, chemist, and physicist, and must master the depths of each of these sciences.

In looking so far into the future, with its unlimited possibilities, we may well repeat the words with which our great teacher, Carl Ernst von Baer concluded the preface to his *Embryology of Animals:* "Until then there will still be a prize for many. The palm, however, will be carried off by that fortunate one for whom it is reserved to refer the active power of the animal body to the general laws of life of the world whole. The tree from which his cradle will be fashioned is not yet planted."

INDIVIDUAL DEVELOPMENT AND ANCESTRAL DEVELOPMENT

BY WILLIAM KEITH BROOKS

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NEAR the end of the last century, zoölogists of a speculative turn were asking whether the changes that make up the history of species are induced by the external world, or are inherent in germ-cells and the living beings that arise from them. We had been told by Haeckel that the inheritance of acquired characters is a necessary axiom of the monistic creed, and, by Weismann, that acquired characters never are, and never can be, inherited, because the architecture of germ-plasm forbids.

So the dispute went on, in the good old *a priori* way, with no sign of any end except an armed truce, until wise and prudent zoölogists resolved to stop disputing and get to work.

One of the fruits of this resolution was a wonderful series of observations and experiments upon the behavior of eggs and embryos under abnormal conditions, the results of which are so instructive, and so full of food for reflection, that they mark an epoch in the history of embryology, making one of its most notable chapters. In so far, the resolution to cease from arguing, and to get to work, has been altogether good, although one need read but little in the current literature of embryology to find that we have not succeeded in laying aside speculative questions. Many embryologists are now asking whether the cell-differentiation which takes place during individual development is inherent in eggs or their chromatin, or induced by the interaction between the constituents of the egg, and between cell and cell, and between the developing embryo and the external world.

The dispute that was laid aside as vain and idle was whether the development of species is inherent or acquired. The new question is whether individual development is innate or superadded; but the distinction is only a verbal one because that which is true of individuals is also true of them when considered collectively.

Some embryologists tell us that each cell that enters into the composition of a multicellular organism is a complete representative of the species, having the same constitution and the same significance in inheritance as the fertilized egg; that each cell has the constitution which is characteristic of the species; that it might, under proper conditions, have become a germ-cell, or any one of the various cells of the body, because the substance of inheritance is transmitted equally to all cells.

According to another view, a germ-cell is the only complete and independent representative of the species, since the substance of inheritance is held to be contained, in its completeness, in no cells except those that are predestined to produce new organisms, while the ordinary tissue-cells are held to be absolutely and inevitably out of the line of descent to future generations, because they contain only so much of the substance of inheritance as is necessary for transmitting the hereditary characteristics of these cells and their predestined descendants.

I believe that a little study of the word inheritance will show us an easy way out of these paradoxes, and I do not believe I could make a better use of my hour, or one that would do more to promote research in embryology, than to point out how far the dispute is a verbal one. So far as the word is used inductively, it means the resemblance of child to parent, of descendants to ancestors, while the difference between child and parent is called variation. These words are also used, metaphorically, to designate the cause or the explanation of the resemblances and differences between descendants and ancestors, just as gravitation is used metaphorically to designate that which makes things gravitate, and geotropism that which makes roots grow downwards, and selection that which brings about survival in the struggle for existence. In what I have to say, I shall restrict myself to the inductive meaning of these words, for I know that your minds and your words are so free from the bonds of metaphysics that you know we accomplish nothing by asserting that heredity makes beings inherit, or that variation makes them vary, or that selection selects.

Let us, therefore, consider the word inheritance as a term to designate the resemblance between parent and child. You all know that while the descendant does, on the average, resemble its ancestors and collateral relatives more than it resembles anything else in nature, it is never identical with them. We say, in our careless way, that organisms exhibit specific identity behind, or in spite of, their individuality, when we mean that, while they resemble their parents, they are different from them. This diversity in unity is true of all natural objects, but it is most notable and impressive in familiar living beings, in our friends and acquaintances, in our dogs and horses, and in the plants that we tend with our own hands. We may think of the casual stranger on the street, or the unknown citizen of Timbuctoo, or the stalks in the corn-field that we pass in the train, as representatives of species, and nothing more, but all the living beings that we know practically, we know as individual members of their kind. We may, for our own purposes, and in our minds, consider their kinship apart from their individuality, but this does not show that they are separable in fact. Living beings do not exhibit unity and diversity, but unity in diversity. These are not two facts, but one, and the separation is in our minds, or our words, and not in nature. The delight of intimate acquaintance with animals is due to the inseparableness of their specific unity from their individuality, and our attempts to separate, in our minds, what is not separable in fact, lead us to two narrow and partial views of the facts, two crude and imperfect mental concepts, neither of which corresponds to anything in nature.

All this is familiar, but I ask you to reflect upon it; to decide for yourselves whether it does not mean that inheritance, or resemblance to ancestors, and variation, or difference from ancestors, are only imperfect mental concepts, crude ideas, and not facts; whether the fact is not the individuality in kinship of living beings. Each of you must answer this simple question for himself. I cannot regard them as facts, since they seem to me to be only imperfect ideas of facts; mental states which we have reached by fixing our attention upon a partial and uncritical view of our sensations and perceptions, to the neglect of that which has not interested us nor seemed to concern us.

If you agree with me that resemblance to ancestors does not exist in nature apart from individuality or difference from ancestors, that inheritance is not a fact, but only an imperfect idea of a fact, admitting of correction and improvement by comparison with nature, and in no other way, — if you agree to this, what becomes of the notion of a substance of inheritance? There is, no doubt, a material equivalent for every idea, but the material equivalent for the notion of a substance of inheritance is in the brain of the speculative philosopher, and not in germ-cells. St. Paul says faith is the substance of things hoped for, the evidence for things not seen, but in science the evidence for things not seen is to be sought by using our eyes, and I can discover no basis for the notion of a substance of inheritance except faith, because inheritance seems to me to be a term to designate a narrow and imperfect view of facts, and not itself a fact.

I hope you will not accuse me of opposing the scientific study of inheritance and variation, for nothing is farther from my thoughts. The resemblances and differences between ancestors and descendants are as worthy of study as arithmetic, which has been of inestimable value to mankind, although there is, in nature, no quantity without quality. We cannot make any progress in natural knowledge without fixing our attention upon some narrow and imperfect view of nature, to the temporary neglect of that which does not interest us, but things do not cease to be because we ignore them. The paradoxes into which the biologists fall, in their efforts to locate the substance of inheritance, remind me of the perplexity of the school-boy, who, having tried to add together six cows and nine horses and four apples, wonders whether the result is horses or cows or apples. If he were to attribute the virtue of arithmetic to a substance of numeration, and to wonder whether it resides in apples or in cows, he would be still more like those who speculate about the location of the substance of inheritance.

If you choose to declare that my contention that inheritance is not a fact is a metaphysical subtilty, I cannot help it. Call me a metaphysician if you will. Hard words cannot hurt me, nor need they scare me. But may it not be the speculative zoölogist, who hunts in germ-cells and in chromatin for the material support of the imperfection of his ideas, who is the real metaphysician, and not I, who plead for nothing but the correction of our judgment, and its reduction to exactness, by comparison with nature?

Some embryologists tell us that all the cells that enter into the structure of a multicellular organism are inherently identical with each other, and with the fertilized egg, in their constitution, and in the possibilities of their development. Each, we are told, might have replaced any other if it had been exposed to the same conditions, and might have become a germ-cell under proper conditions. According to this view, cell-division is always division into parts that are identical with each other, and with the cell that gave rise to them, and it is only because they are exposed to different conditions that cells become specialized and differentiated during development, and not because there is any inherent difference between them. According to this way of looking at individual development, any attempt to account for it by the imaginary architecture of the germ or of its chromatin is idle, because the architecture of the organism does not exist in the germ, since it is the resultant of the reciprocal interaction between the germ and the developing embryo with the conditions of their existence. You will permit me to say that, with certain qualifications and reservations, this view of the nature of individual development commends itself to me as a step in the right direction. The correlation between the normal development of one part of the body and the development of other parts is a familiar fact. The changes that take place in the habits and the plumage of certain birds, as the reproductive organs become functional on the approach of the breeding-season, are known to all, as is also the arrest of these changes when the reproductive organs are removed or aborted by disease. The awakening of the body into full and rounded perfection which comes with the functional maturity of the reproductive organs is so notable in our most familiar mammals that it has come to be regarded as the typical illustration of the correlation between developmental changes in one part of the body and similar changes in other parts, although this is, no doubt, an important factor in all development. Other well-known facts, such as the development of a bud into a leaf-shoot under certain conditions, and into a flower-shoot under others, lend support to the doctrine that there is a correlation between the history of each cell and its interactions with other cells, but the doctrine that cell-division is always division into like parts, and that it is the internal environment of each cell that calls out one of its possibilities and leaves the others latent, is not in itself an answer to the question why, as the egg develops into an embryo, its cells find themselves in a little world of their own making, which is so much like that in which their ancestors developed that the end-product is an individual fitted for the normal life of its kind.

This seems to me to be the real problem of embryology. The external world of a hen's egg in an incubator is the same as that of the duck's egg beside it. So far as the duckling and the chick owe their fitness for the world into which they are to be born to mechanical conditions, they must owe it to conditions which they find within the egg, or make there for themselves, through their own activity as living beings. So far as the nutritive and chemical changes that go on in the hen's egg, the effects of gravity and pressure, of the interaction of cell and cell, of organ and organ, are more like those under which ancestral hens developed than they are like those under which ancestral ducks developed, this must be due to a characteristic difference between the interactions of a chick and those of a duck. While it is, no doubt, in the interaction between the living organism and the world around it that life consists, this does not, in itself, tell us why the internal environment of the cells of the developing chick is so much like that of ancestral embryos that the end-product is fitted for the life of fowls.

The hypothesis we are considering is inadequate in so far as it fails to consider the truth that the development of the chick, or that of the human infant, or that of any other organism, is a preparation for a test that is to come later, in the struggle of life: since the most significant fact in the reciprocal interaction between the developing organism and its environment is that it is a preparation for its interaction, at a later period, with an environment of competitors and enemies. So far as the origin of an individual organism, fitted for the state of life into which it is to be born, is in question, the orderly unfolding, by the interaction between a germ and its internal environment, of all the stages which made up the ancestral environment for epigenetic development, in due succession and order, seems to be more like evolution than epigenesis, unless, indeed, there is something in this interaction which we have not yet considered. Unless we can find an epigenetic explanation of the specific constitution with which the germ begins its development, I do not see how we can account for the facts of individual development from the standpoint of epigenesis.

The hypothesis we have been considering has much to commend it, and it is, no doubt, a step in the right direction. Inasmuch as it emphasizes the familiar truth, so often forgotten by speculative zoölogists, that a living being is no metaphysical abstraction, no self-sustaining, self-sufficient entity, no thing in itself, but a natural body in a natural world, of which it is a part, and with which it is in continual reciprocal interaction, — so far as it carries our vagrant minds back from metaphysics to this great scientific truth, — it seems to me to be altogether good; for the amount of idle speculation which has sprung from neglect of this truth is appalling. I ask your attention to it because I shall have more to say about it. It has been a familiar thought with me for nearly thirty years, not because of any originality of my own, but because I learned it from the study of the *Origin of Species*. I have lost sight of it now and then, amid the paradoxes and perplexities of speculative biology, but I have found them to vanish like mist before the wind so soon as I recalled it; so I ask you to bear in mind, at least for the rest of my hour, that a living being is no self-sufficient whole, but a natural body which is part of a natural world, and that this truth is no metaphysical subtilty, but a fact.

So far as it insists upon, and is based upon, this important truth, the hypothesis we have been considering seems to me to be sound and valuable. Inasmuch as it fails to consider the truth that individual development is a preparation for the struggle of life, it seems to me to be only a partial and imperfect account of individual development.

It is not the only view that has advocates. You know what a prominent place in literature the doctrine of germ-plasm has held. According to this doctrine, individual development is the unfolding of the organization that preëxists in the germ. With qualifications which need not detain us, it is the doctrine that the species resides, in its completeness, in no cells except germ-cells, and that differentiation is due to the differential distribution of the substance of inheritance, each cell being held to receive only so much of this substance as bears its hereditary qualities and those of its predestined descendants. So far as it deals with individual development, its essential feature is the definitiveness of cell-division, for it is based upn the opinion that the ordinary tissue-cells are utterly and completely cut off from posterity because no cell except a germ-cell contains all the hereditary qualities of the species.

I shall not discuss this doctrine in detail, because it seems to me to arise from neglect of the truth that neither a germ-cell nor any other cell is a self-sufficient whole, and because I cannot conceive how a new species can arise if this view is well founded. As is a tissue-cell to a germ-cell, so is a germ-cell to ancestral germ-cells. If tissue-cells are out of the line of descent to new generations, and predestined for their parts in individual history, so must germ-cells be predestined for their parts in ancestral history, and out of the line of descent to anything strictly new; but the notion that the conduct of the breeder of carrier-pigeons and fantails and tumblers was predestined in the germ-plasm of the rock pigeon carries Calvinism to giddy heights that I cannot scale.

Other zoölogists tell us that, since the germ-cell is formed by a process which may be regarded as modified fission, it is fundamentally symmetrical with the body that produced it, and its axes and poles coincident with those of the parent, so that it is practically equivalent to a complete organism from the first, so far as its stereometry or promorphology is in question. This doctrine may, perhaps, rest on a basis of fact, but it gives no account of the stereometry of the parent.

Others, who agree that the organism is a unit, a complete whole, a specific being, from the egg onwards, assert that, while cellular differentiation may enable us to infer organization, it is a serious error to regard it as the measure, or the means, of organization; that the egg is young organism, and not a mere germ that is to become an organism; that there is no qualitative or essential difference between an unicellular and a multicellular organism, between an unicellular germ and the being that arises from it; and that, while complexity increases as development progresses, division into cells is not the means, but only the indication of its progress. There seems to me to be a basis of truth for this doctrine also, but when its advocates tell us that the species is contained in the hen's egg as completely as it is in the hen, their words seem to me to be meaningless, because I have learned from Darwin that the species is neither in the egg nor in the hen, since it is in that reciprocal interaction between the living being and the world around it which I have learned to call the struggle for existence.

Thus the current literature of embryology brings us back to the question we had agreed to lay aside, whether development is inherent in the egg or induced by the conditions of its life.

It may interest you to know what an old question this is. More than two hundred and fifty years ago, that great man of science, William Harvey, declared his intention to "seek the truth regarding the following difficult question: Which and what principle is it whence motion and generation proceed? Whether is that which, in the egg, is cause, artificer, and principle of generation, innate or superadded? Whether is that which transfers an egg into a pullet inherent or acquired? In truth," says he, "there is no proposition more magnificent to investigate, or more useful to ascertain, than this: How are all things formed by an univocal agent? How does the like ever generate its like? Why may not the thoughts and opinions now prevalent many years hence return again, after an intermediate period of neglect?"

Summing up the results of his investigation of this magnificent proposition, which occupied him for many years, he says: "It appears clear from my history that the generation of the chick from the egg is the result of epigenesis, and that all its parts are not fashioned simultaneously, but emerge in their due succession and order. For the part that was at first soft and fleshy, afterwards, without any change in the matter of nutrition, becomes a nerve, a ligament, a tendon; what was a simple membrane becomes an investing tunic; what had been cartilage is afterwards found to be a spinous process of bone, all variously diversified out of the same similar (homogeneous) material."

It is more than two hundred and fifty years since this proof was given that, so far as it is discoverable by our senses, individual development is epigenesis, or new formation, and not the unfolding of the preëxistent; yet, dissatisfied with facts, we go on hunting, with what we call our mind's eye, for an invisible substance of inheritance, holding that development must be evolution in essence, however epigenetic it may appear to sense.

If I venture, at this late day, to point out that ancestral development may be as epigenetic, from beginning to end, as individual development, and that the species for which we are seeking is not, and cannot be, in the germ, I do so because this proof is neither new nor original with me. It is so old that many "up-to-date" zoölogists tell us it is antiquated, abandoned, no longer worthy the attention of advanced thinkers.

According to this view, the species is not in chromatin, nor in germ-cells, nor in differentiated cells, nor in living beings at any stage of existence, nor in the conditions of existence, because it is in that reciprocal interaction between the organism and the rest of the natural world which has been called the struggle for existence. Neither the stability of species nor the mutability of species is in living beings, because it is through extermination in the struggle of life that the type is kept true to its kind, and also through this struggle that it becomes changed.

You will note that it is as great an error to locate species in the external world as it is to locate it in germ-plasm. It neither exists in the organism nor in the external world, because it is in the reciprocal interaction between the two. The biological types, of which those who call themselves statistical biologists tell us, are neither external standards to which living beings approach and from which they recede by variation, nor are they standards fixed in living beings by inheritance.

No two objects, alive or dead, ever are exactly alike, and as we all know that life is a struggle, and admit the diversity of nature, neither the stability of species nor the mutability of species is anything more than we might expect. Inheritance and variation are not two things, but two imperfect views of a single process, for the difference between them is neither in living beings nor in any external standard of extermination, because it is in the interaction between each living being and its competitors and enemies and sources of food and other necessaries of life. It would be idle to seek, within the germ, or in the conditions of its existence, for a principle of inheritance, or for the cause of variation, because species is in the interaction between the organism and its environment.

The specific stability of a growing embryo is no more separable from its individuality than the height of a man is separable from the man. We can think of the height of men without thinking of the men, and we can tabulate statures and treat them by statistical methods, but, while we may, for some purpose that we have in view, withdraw our attention from the men, each height still remains the height of an individual and particular man. So, too, we may tabulate the differences between animals without thinking of their kinship, or we may tabulate their resemblances without thinking of their individuality, but this is no more reason for thinking inheritance and variation are two things than for thinking a man and his stature are two things, or for thinking the head of a man is anything else than a man's head.

Individual dogs are more like other dogs than they are like anything else in nature, and yet one dog is different from another. Is there any reason for thinking the case of cells is any different? Daughter cells may be different, even when they are more like each other than they are like any other cell. The difference between homologous twins and ordinary twins, or puppies of the same litter, shows that germ-cells are not identical, and this is shown, still more clearly, by experiments like those of Mendel. The fact that cells are different is no more proof that they are specifically differentiated than the difference between dogs is proof that the races of dogs were foreordained.

Cell-division may be neither integral nor differential, for the sameness, or kinship, of cells is not philosophical or abstract identity, but practical equivalence in the economy of the organism. When we say two cells are the same in substance, I cannot discover that we mean anything more than our meaning when we say the report of a conversation is the same in substance as the original conversation.

Cell-differentiation is neither inherent in germ-cells nor induced by the conditions of existence, because it is in the reciprocal interaction between them. They who seek it in germ-cells or in chromatin forget that these are not self-sufficient entities, but parts of the natural world. They who seek it in the conditions of existence forget, or fail to perceive, that development is a preparation for a test that is to come later in the struggle of life.

The reciprocal interactions that are characteristic of normal development are of a very peculiar sort. They are not merely actions and reactions, but responses or answers, and I ask you to consider what this word means, because experimentalists often content themselves with a very imperfect concept of its meaning.

If I kick a dog, his actions are not ordinary reactions. They are preparations for meeting the further violence of which the kick is a warning. Events do not take place anyhow and at random in nature. They are so related to each other that each is a sign of others that may be expected in course of nature, and for which scientific knowledge helps us to prepare, but it is the preparation, and not consciousness of it, that is useful. When a chick hears the warning cry of the hen it runs to her for protection from the threatened danger, although it may not know the source of danger, nor even what danger is. There is a relation, external to the chick, between the warning cry and threatened danger, and the effect upon its bodily machinery of the warning is an act which is suited for escaping the danger of which the warning is the sign. Since the danger is not discoverable in the structure of the chick, experimentalists are apt to ignore this characteristic of responses, that which makes them responses and not ordinary reactions; but neither the warning cry nor the danger is to be found in the chick, yet the stimulants which bring about vital responses are thought worthy of study. The ability of the chick to make responses does not restrain it from aimless or injurious acts. Its fitness is not abstract or metaphysical, but practical. It may escape danger by means of its mother's warning, or it may be drawn into danger by an imitation of it, but the bird that falls into the net of the fowler is blotted out of history. Natural selection is not an agent who does things, but a general word for formulating the struggle of each individual for existence, and the survival of the fittest. There is nothing general or abstract in this struggle, for it is preëminently private and particular. We speak of *the* struggle for existence; but my struggle has not been like yours, and *the* struggle for existence is only a formula. Species have come about according to but not because of or by means of the principle of the survival of the fittest, for a formula can do nothing. The fitness of living beings is not ideal or abstract, but private and particular. We say an animal is fitted for its place in nature, although it is clear that the fitness is not in the organism, but in its interaction with its environment. It is dependent and relative fitness, for an external change may make unfit what before was fit.

So far as the development of an embryo is a preparation for the struggle of life, it is like the preparation of the kicked dog for further violence. This struggle is in no way incompatible with the generation of sports and mutations and monsters and abortions and failures, but it is incompatible with the survival of those that fail in the battle of life.

What is true of development as a whole is also true of its successive stages. So far as the interaction between each cell and the internal conditions of its existence is a response to or a preparation for the next step in development, by changes of the same general character as those that take place in the reproductive organs of the bird and modify its plumage, and so far as the sum of these changes fits the embryo for the state of life into which it is to be born, it may survive and have descendants, but the embryo that does not follow substantially the same course of development as its allies is cut off from history.

Since the germ-cells produced by an organism are, on the average, more like those that produced it than like any other germ-cell, they tend to follow a course of development which is practically but not exactly the same. Since the struggle for existence is no philosophical abstraction, no generalization, but a practical matter of personal experience it does not depend, in any way, upon the causes or upon the origin of the differences between the organism that survives and the one that fails. It is therefore perfectly compatible with the evidence that the germ-cells and the other cells of the body are practically alike, and that the differences between them are not inherent, but relative to and dependent upon the conditions of their existence; nor is there any incompatibility between it and belief that all cells and all organisms are practically so much alike that a new animal kingdom might arise, in course of time, from a germ-cell of any modern organism.

So far as the germ-cell from which the new being arises, and the cells that compose the tissues and organs of its parents, and the germ-cells from which the parents arose, are practically alike, and so far as the development of the new organism goes on under conditions which are practically the same, on the average, as those under which parents developed, the resemblance of child to parent, which theories of heredity attempt to explain, is neither more nor less than we might expect, and there is no problem, because all experience teaches that similar bodies act and react in the same way under similar conditions.

The doctrine that individual development is due to the reciprocal interaction between the embryo and its internal environment is inadequate, but when it is joined to the doctrine that ancestral development is due to the reciprocal interaction between the living being and its environment of competitors and enemies, it seems to me to give an outline of an epigenetic account of both individual development and ancestral development: an outline which it will require generations of investigators to expand and perfect. In view of this, is it not time to have done with the pre-Darwinian metaphysical notion of species as something that resides in living beings and is handed down by a substance of inheritance?

SECTION I — COMPARATIVE ANATOMY

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(*Hall 2, September 24, 3 p. m.*)

CHAIRMAN: PROFESSOR JAMES P. MCMURRICH, University of Michigan.
SPEAKERS: PROFESSOR WILLIAM E. RITTER, University of California.
PROFESSOR YVES DELAGE, The Sorbonne; Member of the Institute of France.
SECRETARY: PROFESSOR HENRY B. WARD, University of Nebraska.

THE PLACE OF COMPARATIVE ANATOMY IN GENERAL BIOLOGY

BY WILLIAM EMERSON RITTER

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ANY science is far along on its road of progress when it has clearly defined and correlated its problems, and laid firm hold on the methods by which these may be most effectively worked at. By its problems, I do not mean its few largest, most nearly ultimate ones alone, but as well its numerous lesser ones. And by its methods I have not in mind its laboratory processes only; but as well its intellectual methods, its ways of handling data, of applying principles, and especially its attitudes of mind.

Biology regarded as *a science*, rather than as composed of numerous more or less closely related but still independent sciences, is rather far behind the other physical sciences when looked at from this point of view. Its rearward position is the inevitable consequence of the prodigious complexity of the biological field, and of the recency with which it has come into possession of its great unifying generalizations; and I do not advert to its status with the least suggestion of derogation from the splendor of its achievements, but to emphasize the wisdom of having an occasional "round-up," as we Westerners would call it, like the present, from our many so widely scattered grazing-grounds. The daily work of the cytologist and the paleontologist, for example, are so wide apart that these co-workers are ever prone to forget that they in reality belong to the same fold.

Just here I must take exception to the notion, too widely current, and sanctioned by the place given paleontology in the arrangement of departments and sections for this Congress, that the science of extinct animals and plants belongs to geology rather than to biology. Whatever else paleontology may be, it is first and foremost a department of biology, and is one of its most distinctive and important departments. And while I am in the business of criticising the programme, I must mention another matter, less, however, in the way of fault-finding than for defining or explaining my own attitude toward the topic to which I am assigned. In the division of Biology we have sections of Embryology and Comparative Anatomy. This is in accord with the best views and the best practice; but from my standpoint it is impossible to separate the two, and I cannot consent to discuss the relation of comparative anatomy to biology, and limit myself to the narrower understanding of the term; *i. e.*, to the conception that it has to do with adult structure alone. I must treat it as extending to the later stages of development at least.

It may be remarked here that I do not count myself a professional comparative anatomist, but rather a zoölogist. My working interests are about as follows: comparative anatomy, in the sense above indicated, as furnishing the tools; and general biology as furnishing the standpoint and larger motive for my profession as a zoölogist.

As a final preliminary to my task proper, I must preach a little. This I do with reluctance, because for preaching, except by those called and ordained to the business, I have little taste. But the need being urgent, and the occasion opportune, I proceed, with at least a show of boldness, to preach. The theme of my sermon is a plea for greater catholicity of spirit among biologists. Would that we might never again have hurled at us throne utterances, as it were, on the all-sufficiency of such and such a new method of research; or of the utter uselessness of such and such an old method; or, again, on the all-absorbing importance of some newly found problem, and the unimportance, even insipidity, of other old problems. True, the biological domain is boundless, and the workers in it are human, and hence narrowly limited in power of individual accomplishment. But limitation in strength does not necessarily mean smallness of spirit.

Let not the guilt be on our heads (and by *our* I do not mean the other fellows') of dissuading beginners from going into some particular line of work, embryology or histology, for example, because "it is dead," or there is "nothing more in it." And don't let us cocaine the ambition of a fellow worker in morphology or taxonomy, for example, by such questions as "who cares for such matters?" Attitudes of mind like this do harm, lots of harm. They harm individuals, and they harm science. They are off the same piece with *pathies* in medicine; and "pathies" are bad everywhere. Scientific work done in the "pathy" spirit is pretty sure to be top-heavy and lop-sided; and the scientific man who cultivates a piece of scientific ground in this spirit is quite sure to run off and leave it for some other new piece before he has really found what it will produce. It seems as though we American biologists are rather more given to fashion in our scientific tastes than are those of other nations, though the frailty is by no means a national trait. Think how the phylogeny fashion prevailed a decade and a half ago, and note how strange and alone one looks now who dares be found busying himself with questions in this field. One might about as well be seen at an evening ball in a Norfolk jacket as to venture to touch a question of phylogeny in the presence of an up-to-date biological company. And yet who would soberly contend that problems in this field are without importance, or are all solved, or are insoluble? And the so-called morphological method, why had it such vogue some years ago, and why is it so ignored now? What has become of cell-lineage? Have all the extremely interesting questions that were attracting so much good work a few brief years ago been settled? Why do we hear only an occasional voice from this realm now? How long will it be before the field of regeneration, now so bustling with life, shall be as lone as the temples of Pæstums? Judging from history, long before its problems have been solved. How long will biometry remain in its present high favor? Let us sincerely hope that it will for many and many a decade; while, however, we must expect, relying on history as a guide, that it will soon have to take its place in the garret with the many other out-of-date garments.[1] The burden of my complaining is not at all that we strike out on new lines of work and new methods, and this with enthusiasm and vigor; but that we do this with too much narrowness, with too much contempt for the older problems and methods, and, above all, that we go off and leave them for still newer things before they have been thoroughly tried out. Not only breadth of training, but as well breadth of spirit, is an imperative demand in any science. With benediction on the preached word, we may turn now to comparative anatomy.

One can hardly take up seriously such a question as that of the place comparative anatomy holds *now*, and in the future is likely

[1] Since my arrival in St. Louis, I have been told by an American acquaintance recently returned from Europe that a well-known leader of a school opened a few months ago is expressing the view that "biology ought to be fumigated of statistical method."

to hold in biology, without turning an eye searchingly to the past. If this be done, one's general conclusions cannot escape being largely influenced by what he finds there. When it is found, for example, how many of the largest, most securely established discoveries and generalizations in biology have been reached through comparative anatomy primarily, the general notion becomes strong that the subsidiary science, that in the past has contributed so largely to progress, will continue to be potent in the future. The presumption, at least, this way is strong. It is not my office to review history here, but a few instances will be allowable as giving cogency to the present point. The discovery of the circulation of the blood is usually and justly regarded as a physiological one; yet it is noteworthy that, although Harvey made abundant use of both the experimental and the quantitative methods of research, he still almost always speaks of himself as an anatomist; and the great store he placed on comparative studies is well known. "Had anatomists only been as conversant with the dissection of the lower animals as they are with that of the human body," he says, "the matters that have hitherto kept them in a perplexity of doubt would, in my opinion, have freed them from every kind of difficulty." And the thoroughgoing way in which his practice accorded with his theory, both in his studies on the circulation and on generation, is well known to all familiar with his work.

To Malpighi more than to any earlier biologist belongs the honor of having recognized some of the fundamentally unifying phenomena and principles of the living world as a whole. This he did, more than in any other way, through his comparative researches on plants and animals, particularly on marine animals, during the years of his incumbency of a chair of medicine in the University of Messina.

The true interpretation of fossils, begun by the Dane, Nicholas Stensen, a man remarkable, even in a period so remarkable as that of the mid-seventeenth century, and carried to such brilliant fruition by Cuvier, was, you will recall, strictly a matter of application of the data and principles of comparative anatomy. So one might go on almost indefinitely, instancing epochal advances largely contributed to by comparative anatomy, in aspects of biology not themselves usually counted as belonging to anatomy at all.

The first point of significance of comparative anatomy for biology I am going to notice is that of its value as a discipline, or, more strictly for my present aim, as furnishing a point of view. Be it noted that the biological habit of mind, or point of view, whatever be the phrase that best expresses it, is, as all will agree, essential to healthy enthusiasm and sound accomplishment in biological research; and that this must come through training in and the cultivation of the various provinces of biology. Biology is indeed *a* science, though only from the point of view of its fundamental principles and ideas, not from the point of view of the materials which it furnishes to be actually worked upon. One cannot be a biologist practically, excepting through some of its subdivisions. Now in my opinion there is no single sub-science of the whole biological realm that contains in itself so many of the elements fitted for giving the biological point of view as comparative anatomy. And it seems to me that particularly now, when so much importance is rightly being placed on the experimental and statistical methods of research, it needs to be strongly emphasized that as a method or instrument of research it is the fact of *comparison* that has given and ever must give anatomy its great significance. Right here is one of the points at which my plea for catholicity comes strongly to the front. Some workers in fields recently become so full of promise and so enticing are actually assuring us, in the morning glow of their day of promise, that the comparative method is impotent, and that the future of biology is committed wholly to these new methods! It is assuring, however, to note that a distinguished leader in one at least of the new schools does not hesitate to condemn this sort of thing in harsher terms than I have felt like using.

I would especially mention the importance of comparative anatomy in the preliminary training of medical students. If there be any biologist above all others for whom the biological point of view is of consequence to the general good, that one is the physician. But if the physician is to attain this point of view, he must do it by some other route than his strictly medical studies. It cannot be reached by the study of any single kind of organism. In the main, then, the preliminary training of the prospective medical student must be relied on for gaining the desired end. This is not the place to discuss the matter, but I have reached the conviction that in the United States, at least, that part of the preliminary training of medical students which pertains to the higher vertebrates is, in a majority of our universities, defective. I believe we are drilling on the single type, mammal, too exclusively, and to the sacrifice of what would be practicable and of much greater value in the comparative anatomy of higher vertebrates, the mammals particularly.

The place of comparative anatomy in biology that may stand second in our presentation is that of its significance for systematic zoölogy; or, in the restricted way in which I shall be obliged to treat this head, its significance for determining affinities of the *larger groups of animals*. There can be no doubt that some of the most important, though at the same time most difficult, of biological problems are here. It is probable, too, that fruitless theory has reached its climax in this field. That paleontology is the court of final appeal here for every case that can be carried before it there is no question. Since, however, a class of cases is ever on hand that can never be taken to this court, I propose to make these the centre of consideration, with the understanding, though, that most of the general conclusions set forth have application more or less strictly to other cases as well. I have in mind the problems of the relationships between the primary divisions of the animal kingdom.

It is well to remind those disposed to value lightly efforts to trace phylogenies through morphology and embryology that if we are ever to know the interrelationships of the primary subdivisions of animals, the knowledge will have to be gained from these sources. A well-known paleontologist has lately remarked that "Perhaps the most disappointing element in paleontological results thus far is the lack of all information concerning the origin of the great subkingdoms, or phyla, of animals." (Woodward, 1898.) These results, or rather lack of results, ought not to be counted against paleontology, for, as we now see, paleontology should never have been held responsible for this task: That science is, of course, able to say almost nothing about extinct animals that did not possess hard, imperishable parts. Now, looked at comprehensively, the evidence of paleontology, morphology, and of embryology concur in support of the belief that the phyla of the animal kingdom all had their origin in ancestors *much simpler and smaller than any representatives of these at present known to us;* in ancestors so small and simple, in fact, that preservable *hard parts had not yet arisen.* A well-established skeleton, even of a simple type, must be regarded as always marking a comparatively advanced state of evolution. Thus, even such simple representatives of the cœlenterata as *Dyctorema* or *Diplograptus* of Hallfrom the Silurian must be supposed to have but gradually acquired a sufficiently chitinous hydrotheca to enable them to leave even such remains of them as we have; and consequently, that they must have had a long line of ancestors about which paleontology can never expect to get much direct information. Similarly with the actinozoa, all the evidence we have, both from comparative anatomy and from embryology, leads to the unequivocal conclusion that the coral-producing members of the class acquired the skeleton now so characteristic of them only after a long evolutionary course. Or consider the mollusca. Whichever of the two prevailing theories of the origin of the phylum be favored, constant and characteristic as is the shell, and early as is its appearance in ontogeny, there is no possibility of its being a really primitive structure. In other words, the evolutionary career of the phylum was a long one before this character was acquired. If the turbellaria-like ancestry be the theory advocated, then the evidence from comparative anatomy is positive that the shell is a comparatively recent acquisition. On the other hand, if the trochophore theory be defended, the interpretation of the shell, so well stated by Korsheldt and Heider (1900, vol. IV, p. 323), would unquestionably have to be adopted. "The very early rise of this organ (the shell gland), which may in a few cases be found even before the trochophore form fully develops, must be regarded as a shifting back to an early period of the embryonic development of this feature, which was only a recent acquisition."

So we might go through nearly the whole list of the fundamental types of animal organization and show the extreme improbability, if not the impossibility, that their earliest ancestry will ever be accessible to the paleontologist.[1] This view is of course only the rigorous application of the "Law of the Unspecialized," apparently first definitely formulated by Professor E. D. Cope. That this principle has not been sufficiently recognized at all times by morphologists there is no doubt. The effort to make out the transformation of a Limulus-like arthropod into a marsipobranch-like vertebrate can but be regarded as one of the most extreme cases of disregard of the principle.

It may be held as practically certain that *paleontology will never be able, by direct discovery, to bridge the gaps between any of the phyla of animals.* All it will be able to do in this direction will have to be by inference, and when resort is had to this method, paleontology is worse off than comparative anatomy, since the range of its available data for any particular problem is less. The paleontologist must rest his case on the testimony of a single organ system, the skeletal, while the morphologist has at his command all the systems of organs. True it is that frequently the testimony of the different systems is so conflicting that the difficulty of balancing it up and deciding just what the total signifies is exceedingly great; and in such cases the morphologist is somewhat prone to feel that he has too much, or, rather, too many kinds of evidence; that he could do better could he be rid of some of his facts. But, of course, the paleontologist's seeming advantage here is of a perilous sort. It is similar to that of the systematist's, whose species of plants or animals are beyond question so long as he does not have too many to fit into his descriptions. Since, then, it is by the morphological

[1] I do not forget in this connection the extremely interesting observations made in recent years on fossil remains of soft tissues, as for example, of medusæ (Walcott) and of striated muscles (Dean, 1902). It is, however, hardly conceivable that remains of this sort will ever be found in sufficient abundance and condition of preservation to make them of real importance in the solution of phylogenic problems.

and ontogenetic routes, or not at all, that we must make the passage from phylum to phylum, we are bound to do the best we can with the data we have.

One experienced with some of the problems in this field, and likewise acquainted with its literature, must be impressed by the lack of general guiding principles of procedure; and especially by the lack of criteria for estimating the value of evidence. Several biologists have felt this, and have made praiseworthy attempts to fill the needs. Among these should be especially mentioned Gegenbaur, Cope, Dohrn, E. B. Wilson, Montgomery, and Gaskell. I desire to devote some attention to this topic. The time being so limited as to make it impossible to treat it with any measure of fullness, I merely pick out some of the points that seem to me of most immediate importance for the present state of progress, and tendencies without special regard to their logical order or their coherence.

(*a*) My first point is one of professional delimitation, and attitude of mind, rather than of general biological principles. I state it thus: *We must cease to be embryologists as distinguished from anatomists* when it comes to any particular problem of affinities between groups of animals. Montgomery (1902, p. 225) has recently said: "As to which of these methods is the more correct has been and probably will continue to be a question of dispute. The comparative anatomists maintain one side, the embryologists another, and probably because the former are less conversant with the facts of embryology, and the latter with the facts of adult structure." I suppose this statement of the present attitude of embryologists and anatomists toward one another is true; and I am absolutely sure that so long as it is, we shall not touch solid ground for our general conclusions. What I would insist on is that there is no sufficient reason why it should be so.

True, no one can compass in his personal investigations the whole range of both embryology and comparative anatomy, but that is in no wise essential. All that is necessary is to redraw our lines of specialization. Instead of drawing them *around masses of facts* and *through problems*, as is so frequently done, they must be drawn *around problems*, and *through*, if necessary, *masses of data*. There is no reason why a zoölogist should come to what he would regard as a final opinion on the relationship, for example, of the mollusca and annelida without having himself examined with equal thoroughness the facts of both anatomy and embryology bearing upon the question.

Having reached a position where we might use the facts of development and adult structure with equal facility and equal favor, we should certainly find that in nearly every problem of phylogeny, development must be relied on for light in certain places, whereas adult structure will be the safer guide in others. Fifteen years ago Gegenbaur said, speaking as a comparative anatomist: "Ohne die Kenntniss des letzeren [*i. e.*, adult structure] wie die Anatomie ihren darstellt, würde die Ontogenie sich auf gleichem Wege befinden, wie der Wanderer der sein Ziel nicht kennt."

More recently Driesch, and still later E. B. Wilson, O. Hertwig, and others, coming at the matter from the embryological side, have insisted upon the importance of what Driesch has aptly styled the prospective value of parts of even the very early embryo, in questions of homogeny. With the common truth underlying these two formulations firmly grasped; and with the principles of developmental mechanics thoroughly applied to embryology and comparative anatomy alike, through both experiment and the study of nature's own experimenting, one might confidently predict good progress for the future in deepening insight into the past evolutionary career of the animal world.

My remaining points, more than the first, are attempts to state certain general biological principles that may serve as more or less reliable guides in handling isolated cases. I earnestly hope, however, to avoid the misfortune of being understood to suppose that I have discovered any laws that run on by some mysterious power all their own, bending the incidents of animal structure to their own ends, whether or no. All, of course, I am attempting is to formulate the concordant results of numerous widely separated observations. If there is anybody in the world who has reason to be skeptical of the invariableness of laws in the realm of living things, it is the zoölogist.

(*b*) My second point, then, has to do with what was called by Cope the "Law of the Unspecialized;" and also with the law or principle of change of function, first brought into prominence by Dohrn. It may be stated thus: *The probability that an organ or part in one group of animals has arisen from another in another group by change of function, is inversely proportional to the degree of specialization of the supposed ancestral organ or part.*

I cannot but believe that had this generalization been clearly before the minds of several zoölogists who have in recent years advanced theories as to the origin of various groups of animals, they would never have become sponsors for views with which they now stand credited. One may instance Dohrn's attempt to derive the vertebrate copulatory organs from annelid gills; and any number of Gaskell's laborious efforts to show that the various organs of the vertebrate have been derived from organs highly specialized for *wholly different functions*, in the supposed arthropod ancestor. The rôle of comparative anatomy in applying this principle is obvious. Grade of specialization can, of course, only be tested by considering *adult structure*. And while the indispensability of comparative anatomy is clear, it is well to note again how causal morphology would join hands with comparative anatomy here. To recur to the example of the supposed origin of the copulatory organs from gills: Due consideration for the functional demands of these two sorts of organs would lead to recognition of the extreme unlikelihood of the transformation of the latter into the former.

(*c*) My third effort at a guiding generalization takes the following form of statement: In attempting to find the origin of a given type of animal organization *foremost attention should be given to the organs and parts most characteristic of the type, since the discovery of the origin of these would be most decisive for the origin of the type itself.* Thus, could the view be fully established that mammalian hair originated from epidermal sense buds like those found in amphibia, this would be the strongest sort of evidence in favor of the view that the ancestry of the mammals runs back to the amphibia. Again, this principle would dictate that search for the origin of the mollusca should be particularly promising in investigations on the phylogeny of the mantle, and the shell gland. It would seem as though this principle is so obvious that it should have elicited the regard of every student who inquires into the relationships of larger groups, at least; yet it is surprising to find how largely it has been neglected. Theories of the origin of the chordata, for example, are, several of them, almost wholly wanting in any serious attempt to find how one of the very most characteristic things in the chordate type of organization, viz., the axial skeleton, arose. Of course a corollary to this principle would be that organs and parts merely occasional and incidental within a given group (unless they can be proven to be rudiments) can have but slight significance for the affinities of groups as wholes. Thus it is really surprising that an investigator with the store of learning that Gaskell possesses should have so nearly set at naught his own theory by a complete disregard of the principle. This author supposes, and goes to great pains to prove, that the tubular muscles of ammocoetes are derived from the veno-pericardial muscles of limulus and scorpions. And he tells us this is "the strongest argument in favor of my theory." In a word, the strongest argument Gaskell has in support of his view as to the origin of one of the largest, most distinctly circumscribed phyla of the animal kingdom, rests on an obscure group of muscles found only in the larva of one small division of this phylum!

The importance of comparative anatomy for the application of this principle is likewise obvious enough. It must be the chief reliance for determining the constancy of a part through a series of animals.

(*d*) The fourth and last principle that I here present is one which, while it belongs mainly to the province of comparative anatomy and embryology, laps farther over into the field of developmental mechanics than any of the others noticed. I may say, too, that I have found less suggestion of it in the writings of other zoölogists than I have of the preceding ones. I state it as follows: The reliability of an organ or part as evidence of genetic relationship is *directly proportional to the unlikelihood of its having arisen independently within the limits of the groups of animals being compared;* and the test of unlikelihood of di- or polyphyletic origin of a part is the *number of more or less distinct elements that enter into its composition*; or, what amounts to about the same thing, *the complexity of the part.* To illustrate: Were .paleontology to discover structures in Silurian strata, one kind of which would be allowed by all to resemble closely mammalian hair, and another kind as closely to resemble avian feathers; and should there be an entire absence of direct evidence as to the creatures these structures belonged to, the feather-like structures would furnish stronger presumption of the existence of birds in Silurian times than would the hair-like structures of the existence of mammals in the same epoch; and this on the strength of the evidence itself, and without appealing to any collateral considerations, like, for example, the fact that the general course of evolution makes it probable that birds originated earlier than mammals. The stronger probability attaching to feathers would be due to the much greater complexity of feathers than of hairs, this making it less likely that feathers should have arisen more than once. Or, again, the complexity of the ambulacral system of echinoderms diminishes the probability that such a system would have been elaborated more than once, and consequently its presence in any sort of an animal, however generally unlike any known echinoderm, would still be strong evidence of kinship with the echinoderms.

Inadequate as has been my treatment of the rôle of comparative anatomy in the investigation of problems of affinity, still less adequately am I able to deal with its significance for other groups of problems. Its relation to the various aspects of experimental zoölogy, for instance, is intimate and vital. The best thing I can say in this connection is that, were it my office to prescribe the qualification that should be exacted of all who would go into experimental morphology, for one thing I should insist upon thorough familiarity with Roux's *Problems, Methods, and Scope of Developmental Mechanics*, which introduced his *Archiv* to the biological world; and further, I would exact unqualified accord to that portion, at least, of the essay that sets forth the author's views concerning the relation of developmental mechanics to the several older biological disciplines.

Certain it is that nothing fuller of promise has come into biological science for many years than the set of tendencies in ideas and methods of investigation that have crystallized into the expression "developmental mechanics." It has sometimes seemed to me, though, that the alternative term, causal morphology, would have been more fortunate. The kernel of the thing is, as I understand it, search after the causes of the form of organisms; or really causes of morphogenesis.

Now where does anatomy come in here? Why, in the first place, it is anatomy, is n't it, that shows us what it is we are seeking the cause of? A rather important preliminary to explaining a thing is to know what we are going to explain. Anatomy, then, in the first place, is the source of supply, so to speak, of the very problems developmental mechanics proposes to solve. But has anatomy exhausted its usefulness in this direction when it has handed out the raw material of a lot of problems? By no means. The moment anatomy becomes seriously comparative, that moment it is on the threshold of causal morphology; for as soon as parts obviously homogeneous, but with *considerable differences*, are recognized in different groups of animals, a *differential* in the producing cause of the common part must almost of necessity be assumed by the observer; and since this differential will usually be closer at hand, so to speak, than the cause itself, it is pretty sure to stimulate inquiry as to what the cause has been. And even this much, general and vague though the effort may be, is undoubtedly on the high-road of search after causes of animal form. To illustrate: One's knowledge of the anatomy of the human limbs, let us say, may be complete; but the causes that have produced these limbs are so complicated and obscure, that even were he, as a human anatomist pure and simple, to raise the question of how they came to take the form they have, the absence of even a starting-point for an answer would be apt to prevent an effort in this direction. But now let this anatomist add to his knowledge an acquaintance with the structure of the limbs of, say, a spider monkey. He could hardly escape recognizing that the difference between the limbs of the two animals is connected causally with the different uses to which they are put by their respective possessors. In other words, the cause of the *difference* in limb structure, being relatively near by and simple, can hardly escape him. He is *forced*, almost, by comparative anatomy, into the way of causal morphology, or developmental mechanics. But we must recognize that observation, however extensive and painstaking, and however faithfully and thoroughly it be coupled with comparison, and with reflection on the causal efficiency of function, of correlation, of conditions of development, etc., must always still fall short of direct proof of the cause of the form. Conclusions from this method must usually be presumptive. Hence we must wherever possible call experimentation to our aid, for this is preëminently the method that yields evidence direct and immediate. But here again we must recognize limitations. Undoubtedly there is a wide range of form and structure that lies wholly beyond the reach of direct experimentation. How, for example, can we hope to touch, except perhaps indirectly and from afar, such a problem as that of the phylogeny of mammalian teeth? It is quite possible that experiments on the developing teeth might be made, as, for example, by depriving the embryo of salts necessary to tooth substance; or by artificially altering the pressure on the incipient teeth in some of the marsupials whose embryonic life is largely extra-uterine. But with all the necessary complexities of manipulation, and with the wide scope of inference that would be necessary to determine the bearings of the results of such experiments, I do not see that this method can be expected to yield results for the problem as trustworthy as those that may be looked for from comparative embryology. And the same thing must, it seems, be true of very many problems presented by the higher animals especially.

I should like, did time permit, to say something on the part comparative anatomy must play in the, to me, wonderfully enticing field of animal ecology. But I must forbear.

I may state the essence of this paper thus: From the point of view of its *problems* rather than of its *materials* and *methods of research,* the great biological field is indeed one. Its essential unity can be realized and preserved, and these problems most effectually worked at, by drawing the lines of specialization around *problems* rather than around *masses of facts.* By this procedure we should be led to appraise more justly methods and facts, and should be compelled to see the necessity of employing any and all of these that might help us on our way. Comparative anatomy ever has held, and ever must hold, both for its methods and its substance, a place of foremost importance in biological research. It, along with embryology, which indeed it must include so far as concerns later stages of development, is one of the surest passports of training to the biological point of view.

It is of primary importance in furnishing and applying criteria of the value of evidence in problems of affinity, of phylogeny, and hence of classification.

It is, in both its methods and substance, of great importance to Developmental Mechanics.

COMPARATIVE ANATOMY AND THE FOUNDATIONS OF MORPHOLOGY

BY YVES DELAGE

(*Translated from the French by Robert M. Yerkes, Harvard University*)

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LIKE those of nearly all branches of knowledge, the first rudiments of comparative anatomy are as old as man himself. Ever since he has been able to reflect and observe, even before he knew how to speak, man has carried on the study of the majority of the sciences or of their applications. He studied astronomy the day he noticed that the sun rose each morning at a point on the horizon and that it set each night at an opposite point, and that he could expect the repetition on following days of the same phenomenon; he studied arithmetic as soon as he could count the warriors of his tribe and the sheep of his flock; geometry when he could draw the boundary of a circle by means of a cord attached to a stake; physics when he succeeded in lighting a fire by striking two flints or by rubbing together two pieces of wood; chemistry, and of the most delicate kind, the first time he raised bread-dough with sour dough of the preceding day. In the same way he began comparative anatomy when he gave the same name to similar parts of different beings, when he called the extremities of the horse as well as of the dog, "feet." All the general terms of anatomy, such as head, tail, horns, hair, liver, heart, etc., have for their preliminary condition data of comparative anatomy, defaced and intuitive if you please, but clear and positive nevertheless.

This kind of rudimentary comparative anatomy, which has for its basis a collection of resemblances of such a nature, recognizable off-hand without intellectual effort, has not progressed since ancient times, and persons who have not made a special study of them are, in this respect, at about the same stage as our ancestors of old.

Comparative anatomy could but slowly depart from this intuitive phase. In order to become a true science, it was obliged to wait until another science from which it borrows its materials for study, zoötomy, was established. For the latter is a science which does not impose itself upon the attention of man. By reason of its utilitarian character, human anatomy, "anthropotomy," was studied first, by medical men, and zoötomy only by chance, for the sake of the aid it was able to furnish to anthropotomy by comparison of the structure of man with that of animals. On that account zoötomy has wrongly been called comparative anatomy, and even in our day some people still consider comparative anatomy as being only the anatomy of animals compared with that of man; they confound it with zoötomy, which conception is most inaccurate.

True comparative anatomy has for its first object the presentation in another grouping of the facts of zoötomy and the comparison of them among themselves.

Zoötomy describes the arrangement and structure of all the organs in each animal, and passes in review successively all animals; it gives a complete and concrete picture of the organization of each one. Comparative anatomy studies in all animals successively the position and structure of a given organ, and proceeds thus successively with all the organs; it gives a complete but abstract picture of the constitution of each one throughout the animal kingdom. It is, therefore, not creative; it only points out from another point of view the facts which zoötomy has already made known. In that sense it is not, properly speaking, a science. It is not, however, less useful, and one is wrong to slight it on the pretext that it has not an independent personality in the general tableau of the sciences. It enlarges the views of the anatomists, determines a multitude of ideas, points out new aspects of things. It is the necessary complement of zoötomy, and no one may be a perfect anatomist, if, after having studied zoötomy, he does not review from the standpoint of comparative anatomy the ideas acquired in that study in order to study them anew.

This first object of comparative anatomy is not considered by anatomists as the most important, or as that to which this science owes the high dignity with which they invest it. It pursues another aim more elevated and more difficult to attain, but also more meritorious: the discovery of general laws which may be deduced from the comparative study of the structure of animals. There comparative anatomy is creative, for zoötomy alone could not pretend to the discovery of these laws; it becomes a true science having its own object. It remains dependent upon zoötomy for the materials which it borrows therefrom, but it is no longer content with retouching, with rearranging its facts; it draws from them new conclusions.

Here, as everywhere in biology, these so-called laws cannot be considered as directive principles, as active forces, but only as general propositions summarizing a large number of the facts of observation. The following are the most important of these propositions:

Law of connections. If we compare the characteristics which the same organ presents in a more or less extended series of animals, we perceive that these characteristics are more or less variable according to their nature: color and form are in general very much so, structure, the relations of contiguity, are fairly so; but there is one which is almost invariable, and that is connection, or, in other words, the relations of continuity. For example, the pelvic fins of fishes called jugulars are greatly displaced, since they are carried in front of the pectoral fins, but the nerves and arteries which they receive are given off, nevertheless, from a point situated behind that from which the nerves and arteries of the pectoral fins start; the lungs of serpents elongate to form cylinders which are placed one behind the other, the posterior far towards the rear of the body in a region very different from that which it occupies in other animals; but their point of insertion in the pharynx, the glottis, remains unchanged; the statocysts of lamellibranchs are situated in the foot, far from the place which they occupy among the other mollusks, where they are near the cerebral nervous centres, but their nerve connects them with that centre, a direct emanation of which they therefore remain. This principle of connection is equivalent to considering organs as attached at a fixed point, which is their place of origin, by an elastic cord, which allows them to make all changes of place without losing their connection with the fixed point. This cord is a thread of Ariadne which permits regaining the point of departure despite the most distant migrations. In tracing back these organs among all animals to the place of origin which their connections indicate, an important share of their differences is made to disappear, and their comparison is made clear. This is the principle of Geoffroy Saint-Hilaire.

Principle of the balancing of organs. It is well known that the relative development of organs in the body is very different among different animals. Geoffroy Saint-Hilaire remarked that, when one organ attains an excessive development, one or more of the others suffers a corresponding atrophy. This principle results from the fact that the necessities of nutrition do not allow a number of organs to function at the same time with an activity greater than the average. If certain ones have a very great activity, they develop beyond measure, but, correlatively, others become relatively inert and atrophy.

Principle of coördination or of correlation. As far down as life is possible, there is every necessity that organs and their functions should be bound together among themselves by mutual relations, in a manner analogous to the wheels of a mechanism. Thus it is that the elk could not carry the enormous weight of his antlers unless the muscles of his neck had undergone a considerable development. Other correlations, without resulting from physiological necessities quite as rigorous, appear like the expression of very general provisions. For instance, mammals which have hoofs are herbivorous and have a large and flat maxillary condyle, and teeth with a large crown striated with a crest of enamel, in order to triturate plants as if between millstones; carnivores, on the contrary, which have large canines, have a transverse condyle and a foot with five digits provided with nails. It follows that it is possible, to a certain extent, and sometimes with remarkable precision, to deduce the formation of certain parts by that of certain others; seeing the canine tooth of a lion, the hoof of a horse, the antlers of an elk, we may divine the transverse condyle and the clawed foot of the first, the flat condyle and molar teeth of the second, the powerful cervical muscles and the cervical vertebræ with high apophyses of the third. It is to Cuvier that we owe this principle and its chief applications, and the same author's principle of the *subordination of characteristics* is but another expression of the same view.

Principle of the division of labor. The general functions which organisms must fulfill in order to live and reproduce their kind are the same from one end to the other of the scale of beings. Simple creatures which occupy the bottom of the scale fulfill their functions almost without organs. The substance which constitutes their bodies, protoplasm, possesses the rudiments of all the indispensable properties; it assimilates and excretes, it feels, it moves, it divides. As we mount towards organisms more and more perfect, we perceive that the progressive perfecting has for its foundation the formation of special organs more and more differentiated, better and better fitted to accomplish in a more perfect manner a special work, and less and less capable of performing multiple functions. Thus the motile and nervous functions are divided between two very different elements, the muscle-cell, possessing an energetic and rapid contractility, but insensible, and the nerve-cell, incapable of energetic movement, but well suited to receive impressions and to transform them into motor impulses.

This principle, brought to light and developed with much skill by H. Milne-Edwards, belongs as much to comparative physiology as to comparative anatomy. It is very general, and is verified among all living beings, both animals and plants. Certain facts are in a way corollaries of it. Thus, organs, even those which are specialized with reference to a given function, may be numerous among lower beings, and have a tendency as soon as and in proportion as an organism perfects itself, to be reduced to a pair, or even to one. Thus the locomotor members, so numerous in the annelids and myriopods are reduced to four pairs in the arachnids, to three among the insects, to two in the vertebrates, and to one pair in man.

Principle of the change of functions. This principle, due under this name to A. Dohrn, to whom also we owe the demonstration of numerous applications of it, had been clearly formulated by H. Milne-Edwards under the name of the *principle of physiological borrowing.* He points out that when a new function becomes established, it at first borrows its organs from parts already existing, which change their functions to those to which the modifications correlative with the change have made the organs exactly appropriate. Examples of this are innumerable. One might cite the pectoral fin of the whale, which is only its anterior limb transformed; the poison-gland of the viper, which is a salivary gland; the copulatory appendages of the crab, which are modified abdominal feet.

It is evident that for the establishment of the majority of these laws comparative anatomy calls upon comparative physiology, and it is even noticeable that the most suggestive laws, those of Milne-Edwards, for example, are more physiological than anatomical.

There is, however, one last principle which comes wholly from anatomy, and which is proving itself more rich in consequences than all the others united. It may be remarked, in fact, that the number of these general principles is very limited, and it seems as if there were not many more to be discovered. If it were limited, therefore, to the second object, comparative anatomy in having acquired the dignity of a science, properly speaking, could not be considered a very fertile science.

The principle to which I allude is the following:

Principle of the uniform constitution of animals. A glance at the organization of beings suffices to show that their structure presents striking resemblances. All mammals have mammary glands and hair, all birds have feathers and wings, all vertebrates have limbs and a bony skeleton, the majority of animals have a stomach, an intestine, a mouth and an anus, muscles for motion, a nervous system to control these muscles, sense-organs often quite comparable, a circulatory apparatus, etc.

This principle is an idea the acquisition of which goes back to the most remote times. Aristotle formulated it clearly. Nevertheless, it has been established scientifically, with the necessary details, for the first time by E. Geoffroy Saint-Hilaire, under the name of the *principle of analogy*.

Extending over the whole of the animal kingdom, it is true only for very general and very vague structures. If we go into details, we find important divergences, and it is only by forcing and falsifying comparisons that we can succeed in establishing apparent analogies between organizations thoroughly unlike. The nervous system of a mollusk has almost no resemblance to that of a vertebrate; the organization of a sea-urchin has almost nothing in common with that of an ascidian; the olfactory organ of a crab does not resemble in any possible way that of a mammal.

It is not the same, however, if, in place of extending the comparison to the whole of the animal kingdom, we limit it to a small number of large groups. It is the merit of Cuvier that he established these groups by means of comparative anatomy; they are the phyla of the animal kingdom.

In any one phylum the organization of all the beings which compose it is truly very similar, and if there are differences, real, various, and profound, they are not incapable of reduction.

This principle furnishes to comparative anatomy a third object; it points out a third aim more elevated than the first two, and more difficult to attain. Here not only does comparative anatomy become an independent science because of this object, but it opens to research an unlimited field. It is no longer, as in its first aspect, the simple complement of another science; it is no longer, as in its second aspect, a science limited to the discovery of some rare general principles; it acquires a new dignity, and it presents itself as so vast that its study will never be achieved.

This third aim of comparative anatomy is the comparison of all the beings belonging to the same type, it is the search for the fundamental conformity under the divergences of detail.

This fundamental conformity makes it possible to conceive for each phylum a type of structure from which is derived, as a modification of the type, the structure of each of the forms constituting the phylum.

If all the organisms of the same phylum are derived from a single type, the organs of each one of them are derived from the organs of the type. Therefore, whatever may be the differences presented by corresponding organs of two members of the phylum, these differences are secondary, accidental, subordinate to a fundamental conformity, and the organs, representing the same organ of the type, represent one another and are homologous.

The chief and the highest aim, therefore, of comparative anatomy becomes the search for homologies. The science of homologies, or morphology, is considered the essential part of comparative anatomy, at once the noblest and the most fruitful.

In the comparison of organs of different beings, Geoffroy Saint-Hilaire and his contemporaries took into account all the characteristics, physiological as well as anatomical. Thus they were not afraid to compare the lungs of mammals with the gills of fishes. To R. Owen is due the credit of distinguishing between physiological and anatomical characteristics; he pointed out that the former furnish only superficial analogies, while the latter form the true basis of homology. Thus the wing of an insect and the wing of a bird are analogous as being organs of flight, but they are by no means homologues, having an essentially different structure, since the wing of a bird is the homologue of the arm of man, for we find in it, in modified form but with similar arrangement, the bones of the arm, the forearm, and the hand, and a goodly number of muscles which serve to move it.

It is evident, then, that morphology depends entirely upon the idea of an animal type. The solution, therefore, of morphological problems depends upon the idea of a uniformity in the structure of beings and upon the significance of types.

Now these conceptions vary. The Deists, and therefore Aristotle, explain uniformity of structure by unity of plan. A creative God created species, and by an act of his will constructed them according to a uniform plan, varying only in details and in the application of its fundamental facts.

The aim of comparative anatomy is to discover this plan, either by the study of animals or by rethinking the thought of God.

Others, in a conception more or less pantheistic, attribute to nature what the preceding had made proceed directly from God. There is still a plan, but an unconscious one, or rather a model, a type, an immaterial entity, unrealized, but which yet controls the realization of real forms as the laws of nature direct the phenomena which are subject to them.

This type is understood in two ways. According to one, it is a prototype, the original form, of which real beings are gradual improvements; according to the other, it is an archetype, the perfect form, of which existing creatures are the repeated models, infinitely various, but always degraded, degenerate.

The aim of comparative anatomy is to find this type and to determine how nearly real forms approach to it.

This conception of types, apparently less childish than that of the unity of plan, has been in fact more troublesome; for, because of its greater philosophical attraction, it has seduced more and higher intellects and has directed their efforts towards an end not less chimerical.

The introduction into biology of the concept of descent has produced an important change: the ideal prototype has become an objective reality in the form of the *ancestral type.* It is certain that two given forms, if, at least, they are not too different from one another, have common ancestors, of which the latest is that one from which they differ least. This latest ancestor is the material prototype from which they have both really been derived. The organs of the ancestor have truly become the organs of the two derived forms as far as we may consider as one and the same thing the organs of one being and the almost identical ones of its immediate descendant. We, then, have the right to say that from the phylogenetic point of view the organs of the later forms represent those of the ancestor, and that those of their organs which represent the same organ of the ancestor represent those of one another. The idea of representation gains body and becomes a reality, and morphology, which is the science of representations, becomes a positive science.

The aim of morphology therefore becomes precise and more positive. It consists in determining homologies, considering as homologues those organs which in the ancestor were represented by a common rudiment.

Morphology, then, has phylogeny as its basis. But phylogeny is not a science of direct observation; it is constructed inductively from the facts of comparative anatomy, of paleontology, and of comparative embryology.

The theme of morphology is, then, as follows: to compare organs which we suppose may be homologues and which belong to two different species, to determine by comparative observations, anatomical, paleontological, and embryological, not all of the characteristics of the ancestor of the two species, which is the aim of pure phylogeny, but the typical constitution of that organ in the common ancestor, and to see whether the two organs have surely been derived from the ancestral type. In that case they are called homologous, whatever may be their differences; in the contrary case they are not homologous, whatever may be their resemblances.

This is the matter in its brutal clearness.

Let us take an example: what, in the foot of the ox, is the homologue of the hoof of the horse? The answer is not evident. A philosopher of nature could well conceive an archetype according to which the whole of the foot of the ox corresponds to the hoof of the horse. But the anatomist dissects these parts and finds only one digit in the foot of the horse while he finds two in that of the ox. The embryologist sees the five digits of the unguiculates shown at first in the horse and the ox; digit number one disappears first, afterwards numbers two and five; the ox preserves three and four; in the horse number four disappears in its turn, leaving only the middle digit, number three. He supposes, therefore, that the ancestors have undergone this progressive reduction. Paleontology when consulted shows effectively that such has been the case, and finally we conclude that the hoof of the horse corresponds to the inner hoof of the ox because they both correspond to digit number three of a five-toed ancestor.

In this order of things, the difference in the method of procedure between those who take observation for their guide and those who, confining themselves only to the powers of the mind, seek to think again the thought of God in order to divine the secrets of nature, is not without analogy to that which is manifested in the science of etymology. During a certain epoch the attempt was made to divine etymologies according to phonetic resemblances and the meaning of roots freely interpreted. What is the etymology of savage? We look and find *soli vagus*, one who wanders alone, the savage living more solitary than civilized man. Any other resemblance equally happy could furnish a different etymology of the same value. But when we set ourselves to study the embryology of words, that is to say, the real history of their successive modifications, we find that savage comes from *sauve ; la sauve*, in the ancient tongue, is a forest, and the name comes from *sylva*, so that *sauvage* comes from *sylvaticus*. This is perhaps less pretty than *soli vagus*, but it has the advantage of being true.

To be just, we must remark that the search for homologies by means of observation is not the exclusive advantage of the partisans of descent.

If the transformists more often call to their aid paleontology and embryology, there is there only a difference in the habitual orientation of thought, and not at all an inherent necessity for a difference in the point of view. The deist could equally well seek in paleontology and embryology indications of the thought of the Creator, and the philosopher of nature could as well look there for the applications of the laws of nature by which he hopes to remount to the archetype. For the former, at least, there are examples. And it is probable that if the transformist idea had never been born, deists and natural philosophers would have come nevertheless to look to paleontology and embryology for the facts capable of demonstrating their opinions.

This extension of the field of comparative anatomy, which borders on morphology, or the science of homologies between similar organs of different beings, is not the last.

Anatomists have dreamed of comparing among themselves not only the organs of different beings, but also the organs of the same being which present a certain similarity, and to seek among them for homologies. To these last have been given the name of general homologies, in opposition to those which we have examined above and which are the special homologies.

Thus we have been asked if the occipital bone is homologous to the vertebræ, the humerus to the femur, the hand to the foot, etc.

For the partisans of the theories of unity of plan, of prototype, or of archetype, the problem of the general homologies does not differ essentially from that of the special homologies. Unity of plan may manifest itself as well in the parts of the same creature as in different creatures. The prototype or the archetype may be conceived as having the hand identical with the foot and the occipital formed like a vertebra. For the partisans of modern ideas, the matter is a little more difficult, for there is no ancestral type in which respectively the hand and foot, the leg and the arm, the occipital and the vertebræ, are represented by single structures, so that the problem for the transformists appears quite as subjective a one as for the philosophers who preceded them. The transformists have succeeded, moreover, in giving to the solution of the problem a certain objectivity, reasoning in the following manner: if the occipital were formed exactly like a vertebra, the foot like the hand, the femur like the humerus, we should not hesitate to consider them as homologous, just as we do not contest the homology of the vertebræ among themselves. If, then, in descending the scale of beings by means of comparative anatomy, if in constructing phylogeny by means of paleontology and embryology, we find beings or stages where those parts which we are comparing are more and more similar among themselves, even to the point of being identical, we should have the right to homologize them; otherwise, not. Thus we have come to recognize that the occipital is not a vertebra, and that the homologue of the tibia is, in the forearm, the radius, although in a superficial examination it would appear to be the ulna, as some anatomists, experts in their science, too, have drawn and described it.

Since we have now shown what comparative anatomy is according to generally admitted ideas and under its three aspects, namely: the presentation of zoötomical ideas in an arrangement facilitating the comparison of organs, the search for the laws of organization, and the search for homologies, we must now go more deeply into our subject and examine the bearing of comparative anatomy, the value of its results, and the solidity of its conceptions.

As far as the first two aspects of comparative anatomy are concerned, we have little to add to what we have already said.

We must recognize that in so far as comparative anatomy limits itself to presenting zoötomical facts in another order, it is not a true, independent science, neither in its foundations nor in its results; it is nevertheless extremely useful, indispensable even in furnishing not only to the student, but also to the scholar, a larger view of things, a greater variety of points of view, permitting more general conceptions.

When it searches for the laws of organization, comparative anatomy, although remaining tributary to zoötomy and a little to physiology for the facts of which it makes use, becomes more independent because of its aim, but it continues to be a narrow, limited science, since the number of general principles which it strives to discover is very limited.

In the search for homologies, comparative anatomy allies itself with embryology and paleontology; thus it gains all its amplitude from the importance and the infinite number of problems upon which it borders. In elevating and enlarging itself, however, does it still maintain its solidity?

Two organs are homologous, we have said, when they are derived from the same organ or rudiment in their common ancestor, but that ancestor is in no case precisely known. When the homology to be sought is easy, one may often determine by induction the ancestral character from which are derived the characters to be compared. Thus, although the common ancestor of the dog and the cat is not known, we may affirm that it had a tail, and that this tail has become the tail of the dog along one line of descent and that of the cat along another; and that, consequently, the tails of the dog and the cat are homologous. This renders no service, however, for the organs are so similar that their homology is evident without any reasoning.

But if one asks what is in man the homologue of the pineal eye of the lizard, the matter is more delicate. The common ancestor of man and of the lizard is not known; we cannot infer anything certain relative to the first appearance of the pineal eye; so the question remains unanswered.

And this is almost constantly the case. Thus, when phylogeny furnishes the required response, the question is solved in advance; again, when the question is difficult, phylogeny remains mute.

We must, then, lower its pretensions, and in place of phylogeny, whose responses would be certain if we only knew them, but which we do not know, we must turn to ontogeny.

The latter also gives answers, not without value, but which are indirect and necessitate an induction into which error may glide. We admit, in general, that when organs are represented at some stage of ontogenesis by very similar rudiments, these organs are homologous, however dissimilar they may be in the adult; and, inversely, that they are not homologous, however similar they may be in the adult, if they are represented in ontogenesis by dissimilar rudiments.

If ontogenesis were a faithful copy of phylogenesis, this reasoning would be admissible. But it is not, and the deviations from the parallelism of ontogenesis and phylogenesis are not recognizable by sure signs.

The examples in proof of this assertion are not rare. Here is one: when the larva of the echinoderms metamorphoses into the definitive form, sometimes it retains the mouth, which is merely displaced by passing to the left side; sometimes the mouth closes and a new mouth breaks through on the left side. From the ontogenetic point of view the mouths are not homologous in the two cases; the homologue of the mouth of one of the forms is, in the other, an imperforate point of the surface of the body.

Is it necessary, then, to say that in two species of starfish, the adults of which present the two cases given above, *Asterina gibbosa* and *Asterias glacialis*, for example, animals as like one another as are the cat and the dog, the two mouths are not homologous, that the representative of the mouth of *Asterias glacialis* is such or such imperforate point on the edge of the disk of *Asterina?* [1]

It seems from all the evidence that the common ancestor of *Asterias* and of *Asterina* had the normal mouth of a starfish, and that this mouth has become the mouth of *Asterias*, on the one hand, and of *Asterina*, on the other, so that phylogenetically the mouths of *Asterias* and *Asterina* are homologous, although ontogenetically they are not. Nevertheless, some morphologists, ready for anything, do not fear to reject this common-sense conclusion, and to declare that the mouth of *Asterias* and that of *Asterina* are not homologous.

But on the other hand many morphologists reject that conclusion, and in other cases, otherwise entirely similar, all agree to take the reverse of that fashion of reasoning.

Among the insects, the embryo shows at the beginning of its development an invagination which appears exactly like that which in the majority of other animals (including the other arthropods) gives rise to the primitive gastric cavity. If it became that cavity, we would not fail to homologize it with the archenteron, but since it develops into something entirely different, the mesoderm, we pass in silence over this homology, thus making an exception to our established principles.

Why do we make such an exception to our principles? Because, in spite of our professions of faith, we do not take as a criterion ontogenesis alone as a copy of phylogenesis. When the ontogenetic homology is too strongly opposed to a certain intimate sense of homology which we have within us, we lay it aside, passing it over

[1] In the same way we refuse to recognize as similar the general body-cavities of two animals, in spite of resemblances which render them almost identical, when one arises as an enterocoel and the other as a schizocoel.

in silence in order not to avow to ourselves the contradictions of our logic. And what is this intimate sense of homology which directs us thus? It is nothing less than the remains of the old concept of the archetype which slumbers in us and wakes occasionally.

When, in two allied forms (the instance is found in the mollusks), the blastopore becomes in one the mouth, in the other the anus (*Paludina*), we might conclude that the mouth of the one is the homologue of the anus of the other. We do not, however, and we are right. But this proves that we do not hold to the criterion which we have erected in our statement of homologies. We abandon ontogenesis, and take for our guide connections and structure, that is, the same characteristics which we declared entirely insufficient to determine homologies if they were not corroborated by development.

After phylogenesis and ontogenesis, it is to connections that we attach the most importance in determining homologies, and very often we content ourselves with them as a criterion. This confidence in connections has its reason for existence in the fact that we know that organs modify more easily their relations of vicinity than their relations of continuity. But it is not wholly founded on observation; it proceeds in part from the conception of an archetype with which our minds are imbued, and from the fact that we conceive more easily of the derivation of that archetype by the stretching and displacement of organs, elastic and pliable after the manner of gutta-percha, than by the transposition of masses in the way one treats the first draught of a wax model.

We must not forget, in fact, that in ontogenesis the mesodermal masses change place thus *in toto*, without maintaining any relation with their place of origin, and that even invaginations, infoldings, detach themselves and become free in order to go and plant themselves elsewhere (imaginal disks of insects, enterocœlic vesicles of the echinoderms, urinary bladder of the vertebrates which becomes detached from the intestine and opens with the ureters, etc.)

Thus, the criterion of homology which, in order to be objective, ought to remain wholly phylogenetic, is almost never so, and it borrows, according to the case, from ontogenesis and from anatomy. And according to the case, sometimes we accept the conclusions to which we are led, although they may seem to clash with the most reasonable comparisons, sometimes we reject them for the same reason.

It must be remarked, in fact, that when the criterion ceases to be directly or indirectly phylogenetic, it ceases to be concrete. That kind of material continuity between the organs of the ancestors and similar organs of the descendants which exists in phylogenetic homologies disappears in anatomical homologies.

When two organs whose phylogeny is unknown resemble one another in certain anatomical characteristics and differ in certain others, if we affirm their homology, that is to say, if we subordinate their differences to their resemblances, we do so only by comparison with an entirely subjective type to which we refer them.

In the construction of this subjective type we have no other guides than certain anatomical characteristics, so that our premises and our conclusions are one and the same thing; in other words, we make a vicious circle.

For example, when we homologize the endostyle of the ascidians with the thyroid gland of Ammocetes and the other vertebrates, we presuppose a common phylogenetic origin for these organs, but since we know nothing whatever of this common ancestor, in reality we conceive of an abstract form in which the endostyle and the thyroid are replaced by one and the same rudiment from which we suppose that these organs are derived.

This abstract form is nothing else than the archetype of the natural philosophers, more refined, more certified, fashioned more by observation, but not less subjective.

The fact is more striking in what concerns general homologies.

No one disputes the homology of the rudimentary mammary gland of man with that of woman. Nevertheless that homology could not in any way be based on phylogenesis. It has been interpreted as a mark of a primitive hermaphroditism, but that opinion is untenable, since the ancestors of man had ceased to be hermaphrodite millions of generations before they were provided with these glands. Here, then, the homology is founded *solely* upon the unconscious conception of an archetype common to male and female based upon anatomical resemblances without any possible phylogenetic significance.

In the vertebral theory of the cranium we do exactly the reverse. We conclude from anatomical and embryological observations that without doubt no ancestor of the vertebrates had a cranium composed of true vertebræ identical with those of the backbone, and we go on from there to declare that no part of the skull, not even the occipital, is homologous to a vertebra.

If, however, the occipital, although developing by the localized ossification of a cartilaginous cranium continued by the addition of a membrane bone, were found to be identical in form with a vertebra of the backbone, would we deny that homology? We should have the right, but we should fall into the same exaggeration as in the case of *Asterias* and *Asterina*.

There is no use in insisting further upon having the right to conclude that the criterion of homology is nothing absolute. We announce our pretension of borrowing that criterion from phylogeny;

as a matter of fact, that furnishes us nothing certain, and we turn to ontogeny and to anatomy, granting more value to one kind of argument or to the other, according to the case, without any fixed rule. In fact, we bring together all that we know concerning the organs whose homology is in dispute, and we proclaim homology when we find between these organs a sufficient conformity of characteristics. In general, we interpose the condition that this homology shall not oppose the idea, very vague, very hypothetical, very individual, which we may have concerning the phylogenetic derivation of the organs under consideration; but in many cases we forget this, and are guided by the unavowed conception of an abstract type constructed according to anatomical characteristics of every order.

The foundations of homology are a mixture in varying proportions of comparative anatomy studied profoundly, of paleontological data too often incomplete, and of a hypothetical phylogeny, together with a dose, not to be overlooked, of that mysticism with which natural philosophers constructed their archetype.

This formula may appear a little irreverent to the devotees of morphology; it is just, nevertheless. If we go to the bottom of things, we must recognize this fact: to homologize is simply to compare, to establish resemblances and differences in characteristics, and to proclaim that these are casual, secondary, while those are fundamental.

Now, there is nothing more delicate than pronouncing upon the comparative dignity of characteristics. There is a question of the orientation of ideas, dependent upon time and place, a question of mode of which it is prudent to be suspicious.

When R. Owen distinguished in the determination of homologies physiological characteristics from anatomical, and established the difference between analogies and homologies, he rendered a real service, for there is always an advantage in not confounding things which are distinct; but it is less certain that he did a good thing when he gave the precedence to homology over analogy in the comparison of characters, for it has led to an exaggerated disdain of physiological characteristics.

When we proclaim an homology like that of the lungs of mammals with the swimming-bladder of fishes, for example, we assume a grave and sententious tone, as if we were filled with a feeling of our own merit in announcing a fundamental truth which remains hidden in a superficial examination. If, on the contrary, we announce an analogy, we take a tone light, and almost a little contemptuous, in order to set off well the small value of a wholly superficial resemblance in which we must not place too much confidence.

Is this right?

Is not this subordination of propriety to substance an effect of the influence which the materialistic conception of the universe exercises upon our minds? Will our sons continue to think thus if the energetic conception, quite as reasonable as the other, if not more so, comes to outweigh it? And we ourselves, should we also be on the affirmative side if we were the spiritual sons of other natural philosophers, who had placed in the first rank in their conceptions not organs, but functions, who had conceived of beings as having to accomplish a series of physiological actions, the nature of the organs by which they accomplish them being of subordinate interest?

Perhaps in that case we should be more struck by the fact that the gill of the fish and the lung of the mammal both serve for respiration than by the difference in their structure and in their material origin.

Is there not also more interest in seeing two organs, otherwise very different both in structure and in phylogenetic origin, coming, under the influence of the necessity to realize functions and by the action of similar surrounding conditions, to have functional and structural resemblances at times astonishing, than in establishing the fact that two organs different in structure have a similar embryonic or phylogenetic origin?

Is the convergence of analogous organs less worthy of respect than the homogeny of homologous organs?

Here are a fish and an octopus. We admit, rightly, without doubt, that they have not a common phyletic origin, or, at least, that their community of origin, if it exists, dates from a stage when their special organs were not differentiated. They both have an eye which, in spite of certain differences, presents a conformity of structure really striking. In spite of their difference of origin and their absence of relationships, the two protoplasms which constitute the fertilized egg of the octopus and that of the fish both develop a specialized organ, an eye, which is remarkably similar in both. In the two phyletic series of the octopus and the fish, under the influence of a fundamental conformity of the substances constituting the organism and of a similar reaction to the analogous surrounding conditions, there are formed these two eyes, which are almost identical, although they are not related.

Examples of this kind are numerous. Here is another quite as striking. Many forms belonging to the groups of the mollusks, of the cœlenterates and the worms have special organs of equilibration, statocysts, consisting of a heavy mass sustained by sensitive hairs arising from the epithelial lining of a vesicle. The crustaceans have on their antennules statocysts notably different in structure. Only one, *Mysis*, has statocysts very similar to those of the mollusks, not on the antennules, but on the telson. This situation prevents our homologizing them with the antennulary statocysts of the other crustaceans, and the difference in phyletic origin prevents homologizing them with those of the mollusks, the worms, or the cœlenterates. Is not a fundamental conformity so profound, between organs phylogenetically distinct, quite as remarkable a thing as the resemblance of origin revealed by embryology between two organs the structure and functions of which are very different?

Is it right, then, to place the latter in the holy tabernacle of homologies in order to prostrate ourselves before it, while we relegate the former to the despised chaos of analogies?

But, some one says, comparisons must nevertheless have a sanction, and homologies must be distinguished from analogies.

That may be, but there is no need to sacrifice the one to the other.

Let us return to the case of *Asterias* and *Asterina*.

When we have proved and noted that the mouth of the one does not proceed from the same point of the larva as does that of the other, we have given to embryology all that it has a right to claim, and it is only just to render to anatomy what it has a right to demand in declaring that in all other respects the mouth of *Asterias* and that of *Asterina* are identical.

In the presence of these divergences, shall we clash with embryology in proclaiming an homology which it rejects, or torture anatomy in denying an homology which the latter claims? The simplest thing is to clash with or torture nothing by saying nothing.

Where is the necessity of formulating a general proposition which shall certainly be false on a certain side, when it is possible to separate it into two true propositions, in saying that the mouth of *Asterias* and that of *Asterina* are similar in all respects except that they are not homogenic.

But, some one says, that is what we do when we declare that the two mouths are not homologues, since by definition homology is nothing else than phyletic homogeny.

That would be true if we held scrupulously to that definition; but as a matter of fact, in the search for homologies we turn to all possible characteristics, even at times to physiological ones, forbidden though they are. We must many times reduce homology to the modest significance of homogeny.

Homology has become and will remain in biological language the mark of an important, fundamental resemblance, reducing to a subordinate and superficial significance and to a secondary interest whatever differences there may be.

There are words which are to ideas what infectious microbes are to the body. Such, in the science of evolution, are "tendencies of nature," "hereditary propensity," "latent characteristics;" in comparative anatomy such are "organs representing one another." Like the phrase in physics, "horror of nature for a vacuum," they correspond to nothing real. Many agree to this, but that does not prevent us from continuing to bring them to the front as if they contained a positive explanation. The progress of ideas lessens their harmfulness, it does not destroy it.

If, instead of proclaiming that two organs are homologues, we should content ourselves with saying that they have the same embryonic rudiment, or similar connections, or a corresponding structure, and that this authorizes us in a certain measure to think that they come from the same rudiment in some ancestor more or less distant, we should say only what we have the right to say, and what would carry with it nothing difficult. It is not the same when we decree a decisive epithet implying that there is something important and fundamental in resemblances, while differences are accidental and subordinate.

There is, without our taking it into account, in this subordination of certain characteristics to others, a remnant of the mystical conception of the archetype. After having made the archetype objective in the ancestral type, most of the time we lose sight of it, and we give a fanciful reality to an entirely subjective type, a simple schematization of abstract ideas. We create mental images of types of organs, of types of structure indefinitely varied and divided up according to the needs of the moment, and we lose sight entirely of the idea of finding the realization of them in an ancestral form previously existing. In each instance we are ready to answer that we are taking the phylogenetic point of view, but most of the time it is not so, and if it should be necessary to sustain that pretension with good arguments, we should find none at all.

This tendency to schematization is not wholly bad. It aids the mind in grouping scattered facts in such a manner that one may consider them as derived one from the other according to simple rules. There is nothing inconvenient in conceiving of types of animals, types of organs, types of structure, as numerous, as varied, as one wishes. But this is so only on condition of never forgetting that they are creations of our minds, without any objectivity, destined only to facilitate intellectual operations. The morphological type must be considered only as an *instrument of thought*, and not as a mystic entity, more or less hidden, which we may by observation and study find again just as it is and not otherwise. We are at liberty to construct it, the only condition being that it shall be advantageous for study and that we shall never take it for anything else than it is.

There must always be present in our minds the fact that an homology is never absolute, that organs *represent* one another in certain respects, relatively to certain categories of characters, and never wholly.

To homologize is to compare. Now, things are never so different that we cannot compare them, nor so similar that the comparison will not be false in some points. The tail of the dog represents almost identically that of the jackal, a little less so that of the ox, a little less that of the bird, a little less that of the serpent or of the fish; it does not represent that of the scorpion or the crayfish, but it would be an exaggeration to say that it has nothing in common with the last two. One comparison is always permissible. When Oken compares the vault of the skull to that of the heavens, there is this in his favor, that one, like the other, is a hollow hemisphere having inside it something which thinks. The mistake is made when we attempt to draw from such distant resemblances consequences more exact or more extended. The mistake is the same, in a lesser degree, when, after having homologized, for example, the radius with the tibia, we imagine, as some of us have a tendency to do, that there is not in one of these bones a single tuberosity or furrow which has not in some more or less hidden form its representative in the other.

What must we conclude from this study?

Comparative anatomy is a science which arranges, classifies, separates, brings together, groups, and labels information, reunites scattered facts under general formulas, compares, finds likenesses, differentiates, subordinates, makes a hierarchy of characters. It is the science of the study, the library, the museum. It borrows much from nature through zoötomy, paleontology, embryology, but it is through meditation that it puts its materials to work. It attempts at times to rise even to the explanation of phenomena, but always in an indirect way and without hope of verification *a posteriori*, in the way in which history explains politics.

It is not a laboratory science.

In that respect it is and it remains a science of the past.

The future, in biology, is for experimental researches, those where one puts on an apron, where one weighs, dissolves, corks up, heats, filters, distends, compresses, shakes, sections, cuts, electrolizes, etc., where one works with substances or with living beings which one submits to physical and chemical agencies or to conditions of life which cause them to vary in a methodical manner in order to produce modifications and thereby to discover, if possible, the causes of forms, of structures, and of their variations.

Does this mean that we must renounce comparative anatomy, and that this science, in which the Saint-Hilaires, Cuvier, J. Müller, Owen, Gegenbaur, and many others have become famous, has no further service to render? Certainly not. It continues to be indispensable to all of those who are engaged in biology in order to diversify points of view, enlarge conceptions, coördinate information, in order to reduce to a small number of essential propositions the multitudes of scattered facts to which it gives a significance and which it causes to converge toward general principles, in order to permit unexpected and suggestive groupings, to show the chief bearing of ideas which seem commonplace or of resemblances apparently insignificant.

As a science explanatory of biological phenomena, it furnishes its share of ideas and facts, but it is not armed properly to solve problems, and allows itself to be distanced by experimental researches in cytology upon the sexual elements, in fecundation, parthenogenesis, ontogenesis, teratogenesis, the action of agents of every kind upon living beings in the diverse conditions of their biology, in heredity, variation, the acquisition of specific characters, and in the nervous functions, from the most elementary sensations up to instinct and to the highest manifestations of intelligence.

In certain works on paleontology the importance of diverse beings or groups of beings at different epochs is represented by the varying width of a band which traverses the successive stages of the geological epochs. If we should do the same in order to represent the relative importance of comparative anatomy in the different epochs of our history, we should have to figure it as a line of extreme thinness traversing the ancient epochs, suddenly becoming very large at the beginning of the last century, and retaining even to our day a respectable amplitude, which, however, does not seem destined to increase indefinitely in the future.

Experimental researches in biology meanwhile would take the form of a triangular band whose summit would be turned down towards the past epochs, while the base, growing larger and larger, will without doubt continue to enlarge during a length of time impossible to foresee and perhaps unlimited.

SHORT PAPER

Professor George Lefevre, of the University of Missouri, read a paper before this Section on "Artificial Parthenogenesis in *Thalassema Mellita*," giving the results of his studies at the Laboratory of the United States Bureau of Fisheries at Beaufort, N. C., during the previous summer.

DEATH OF CAESAR

Photogravure from the Painting by Jean Léon Gérôme.

This is an artistic reproduction of the famous painting by Gérôme depicting in a most dramatic manner the tragic climax to the conspiracy that was formed against Caesar under the leadership of Brutus. The painting was first exhibited at the Paris Exposition of 1867, at which Gérôme was awarded one of the eight grand medals.

SECTION J — HUMAN ANATOMY

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(*Hall* 2, *September* 22, 3 *p. m.*)

CHAIRMAN: PROFESSOR GEORGE A. PIERSOL, University of Pennsylvania.
SPEAKERS: PROFESSOR WILHELM WALDEYER, University of Berlin.
PROFESSOR H. H. DONALDSON, University of Chicago.
SECRETARY: DR. R. J. TERRY, Washington University.

THE Chairman of the Section of Human Anatomy was Professor George A. Piersol, of the University of Pennsylvania, who opened the meeting by remarking:

"Those of us who have listened to the general addresses delivered during the earlier sessions of the work must have been impressed with the breadth and comprehensiveness of the acknowledged purposes of this Congress. These purposes have been not only to bring into touch the widely diverse divisions of science, but also to afford opportunities for exchange of thought between those concerned with problems more or less akin. For, with the ever-increasing mass of details that each year adds in all branches of knowledge, it becomes less and less probable that the single mind can master the minutiæ of more than a limited domain.

"In recognition of the inevitable specialization that the development of science has brought, have been arranged the hundred and more sections of which our own — that of Human Anatomy — is one.

"Human anatomy represents one of the oldest biological specialties, for what more natural than that man's complex organism should have early attracted searching inquiry? But specialization begets narrowness, and this, coupled with the potent influence of the long prevailing views regarding man's assumed exceptional origin and place in nature, did much to retard the establishment of human anatomy upon the broad basis that it to-day enjoys.

The too often well-founded charges formerly made by our brothers, the zoölogists and comparative anatomists, that the human anatomist, ignoring morphological significance, failed to obtain a true perspective in his exclusive studies of man, are, happily, rapidly losing force, as on all sides has arisen a keen appreciation of the necessity and value of regarding man as a member of the great zoölogical family.

"Who shall estimate the stimulating influence of the broad-gauged men who enjoyed the golden age of opportunity during the last century and added so much of epoch-making significance? Among the many, we recall the names of Johannes Müller, Hyrtl, Henle, and Luschka; of Sappey, Owen, Huxley, and Turner; and of our own great fellow countryman, Joseph Leidy. Two additional names of men to whom anatomy owes much must be mentioned: those of His, the sudden ending of whose productive life science even now mourns, and of Koelliker, — the Nestor of anatomy, — who, in spite of his more than fourscore years, still contributes to the science he has so long and brilliantly served.

"In keepingwith the broad spirit of a great international exhibition was the happy inspiration to invite distinguished scientists from across the seas to participate in the sessions of this Congress. And it is particularly appropriate that this Section is to be addressed by an acknowledged leader in anatomy; one whose broad interests and many-sided accomplishments give to his words, written or spoken, an interest and authority universally recognized. I have the great pleasure of introducing Professor Waldeyer, of the University of Berlin."

THE RELATIONS OF ANATOMY TO OTHER SCIENCES

BY WILHELM WALDEYER

(*Translated from the German by Dr. Thomas Stotesbury Githens, Philadelphia*)

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When I attempt to treat correctly, according to the general programme, that branch of science which concerns itself with the study of the structure of our own bodies, let me first recall that here we must create something for life out of death. Even the most long-lived man passes over the stage of the world like a shadow-picture. He passes quickly away after a short instant of existence, "a walking shadow signifying nothing."

But if the life of the individual signifies nothing, the stream of living individuals which constantly flows over our planet shows in man the greatest, the most important, the most powerful being which the world has brought forth, and I place against the words of the great Briton, those of the great Grecian,

Πολλὰ τὰ δεινὰ κ'συδὲν ἀνθρώποι δεινότερον πέλει.

Thus we see that man does not hesitate, in his search for true knowledge of how life springs from death, to lay the hand of investigation even on his dead, in order to learn from them what he is. It has, indeed, cost him centuries of severe struggle, of the building-up of culture, before he attained this. Man has killed his kind without scruple in thousands, in millions, in billions; yes, has boasted of it, and has praised the act in songs and poems, and does still to this day; but before the blank, senseless corpse, the *memento mori*, he felt ashamed. The mutilation of corpses, when it has occurred, has always been severely judged. Even the fame of Achilles has not been increased by the fact that he dragged the corpse of Hector around the holy city. In earlier times the opening of bodies was looked upon as a desecration. This is why human anatomy, although placed among the most ancient studies, was first raised to the rank of a science when investigation of human bodies could be undertaken in increasing number, owing to the powerful efforts of educated men with a determined aim.

I may be permitted, in order to explain more clearly and better, on the one hand, what branches of human science have been assisted by anatomy, and on the other hand, which have furthered it, to give a short sketch of the principal epochs in the course of development of human anatomy.

I think we may distinguish three great divisions of this development. A first, pre-Galenic, which we may also designate in a certain sense as prehistoric, a second, the period of Galenic anatomy, and a third, the period of Vesalic anatomy, which extends until the time of Theodor Schwann and Johannes Müller, 1839, or, in round numbers, 1840. At that time begins the epoch in which we now are.

If I may briefly describe the first period, whose beginning is as unknown to us as that of the human race, anatomy consisted of a sum of unconnected facts concerning the inner and outer parts of the body, such as were obtained from immediate experience and from the observation of the body in its different motions. It was also obtained by the observation of wounds,—note the descriptions in Homer,—and from sacrifices of man and animals. The fact that the human race undoubtedly first appeared in the tropics and subtropics, and at first neither required nor used clothing, permitted observations to be easily made.

That which was so determined and handed down became, with increased culture, more and more the property of the priests, and of the physicians, who were generally of the priestly class. But what we can learn from the Assyrian excavations, from old Egyptian, old Chinese, old Japanese, old Thibetan, and old Indian literary and other monuments is not sufficient to display this historically. Therefore, I use the expression, "prehistoric," because in part their material is entirely false, and nowhere is a complete system brought together. It is merely "anatomic fragments" which we get to know. From them we can form no clear idea of the state of anatomic science of the time under consideration, or to what extent their medical therapeutics was influenced by their anatomic knowledge. There is, indeed, much in the papyri of Egypt and in the voluminous Indian and Chinese literature, but in the short sketch given here, I can only mention it in the above way.

In pre-Galenic times the anatomic knowledge of the Greeks appears to be more accurate. We possess statements that, already before the time of Hippocrates, dissections of human bodies were carried out, and we may assume that among the Indians and Egyptians this was also occasionally the case. We know, however, nothing more definite, and these dissections were certainly rarely performed with sufficient care or with the definite intention of obtaining clear anatomic knowledge. Otherwise, the writings which have come down to us would contain more facts.

The anatomic writings which are ascribed to Hippocrates contain many more facts, and these are much more correct; but, even from them it is plain to be seen that a systematic study of the corpse was not the basis of the facts contained in them. That dissections, especially for anatomic study, were carried out by the Hippocratic school, is open to strong doubt.

From this time on, the slowly collected anatomic data are increased by numerous physicians, philosophers, and naturalists, but even these advances can hardly be referred to systematic dissection of the body. It is especially striking that Aristotle, who had so much at his command, and whom we thank for so much in zoölogy and zoötomy, knew as little about the anatomy of man as is found in his writings.

The data obtained by Herophilus and Erasistratus, who lived between the middle of the fourth and the first third of the third century before Christ, seem to me to show that they were the first who made truly anatomic dissections on the human body. That they opened the body cavities of many corpses is certain, but I believe we may go further and say that they have dissected carefully.

Unfortunately, hardly anything of their writings is preserved, and just as little of Marinus, the precursor of Galen, whose twenty-volume anatomy has only been preserved in Galen's abstract, as have some facts concerning the advances of Herophilus and Erasistratus. Thus it appears to me to be justified to let this epoch reach to Galen.

Galen of Pergamos, who lived in the third century of the present era, was more student and compiler of extraordinary industry than original investigator, but nevertheless he must be placed at the apex of the second period of anatomic study, partly because he brought together everything which had been determined before his time, exercised critical judgment on it, and added to it his own investigations, which, however, were only obtained on animal material, especially apes; principally because the standard of anatomic science codified by him remained authoritative for all the cultured races for 1300 years and more. During all this time his work remained the authority, an almost unique example in the history of science.

Several causes coincide to explain this striking fact. One of these is, of course, the giant work which Galen performed. It seemed built to last for centuries. The principal reason is that man hesitated to lay hands on human bodies, and if in each century a few physicians rose above such thoughts, where could they find a place to carry on anatomic studies? Even a simple opening of the body, "obduction," was not permitted. There were no "Anatomic Institutes." These were reserved for a later epoch. If, occasionally, the opportunity offered for the performance of an autopsy, the deviation found in one or a few cases was not sufficient to shake an authority as well founded as Galen's. For that, a material was required like that on which Vesalius worked, and a mind like his own to interpret it.

Andreas Vesalius (1515 to 1564, his period is usually given, although neither date is certain) and Gabriel Fallopius made a new departure in anatomy. They replaced uncertain data, mostly founded on chance observations and on animal dissections, by systematically arranged observations, based on methodical investigations of human bodies. I name Fallopius with Vesalius, not only because he immediately corrected many false ideas of the latter, but because he was one of the most accurate observers whom we find in anatomic literature, and therefore, in his short life (1523 to 1562) made so many discoveries in the realm of descriptive anatomy that he was equaled by no one before or since, and finally because we have received from him the first orderly attempt toward a general anatomy. As third among the founders of scientific anatomy, Eustachius of Rome, the contemporary of Vesalius, must be mentioned.

Even before the time of Vesalius, comparatively systematic autopsies on human bodies had been undertaken, especially in Italy, and even in a scientific way, and with the agreement of the government. This was the case in Bologna, Venice, Rome, Florence, Padua, and other places. Padua possessed as early as 1446 an anatomic theatre. Vesalius himself, born in Brussels, received the greater part of his anatomic education at Paris and Louvain. Thus we see that the final complete revolution was to some extent prepared for, as new periods always have their dawn.

From Johannes Müller and his pupil Schwann we must date the last period of the development of our knowledge. Men like Malpighi, Morgagni, William Harvey, Albrecht von Haller, and K. E. von Baer, have, indeed, carved lasting marks in the flourishing tree of our science by their brilliant discoveries and well-founded systematic compilation of contemporary anatomic studies, as well as by fruitful comparisons of the same, with allied sciences, but none of these had the same epoch-making influence as Müller and Schwann. The founding of the cell-doctrine by Schwann, 1839, which first made possible a scientific general anatomy and histology, was the most influential. At the same time, through the action of Müller's genius, another spirit was introduced into anatomic descriptions in general anatomy, as well as in embryology and comparative anatomy, of which the composition of Henle's text-book of systematic anatomy on the one hand, and Gegenbaur's work on the other, give proof. At the same time the text-books of histology and general anatomy, as well as those of topographic anatomy, begin to be more numerous; also the special treatises on these subjects, and, finally, the searching investigation of specialists in the anatomy of certain regions begins at this time.

Human anatomy continues to develop itself more and more completely in all these directions up to our own day. We must recognize the branch of human anatomy, and limit ourselves to this branch according to the following scheme:

(1) Descriptive anatomy of the human body.
(2) Topographic anatomy of the human body.
(3) General anatomy.
(4) The anatomy of different ages of man from the first development until natural death caused by old age.
(5) The anatomy of the human races in all these relations.

All these must receive scientific enlightenment from the general history of development, as well as from comparative anatomy of that branch of animals to which man belongs physically, the vertebrata.

I may be permitted to make here an explanatory observation. We must distinguish sharply, as is not always done, between general anatomy, histology, or the study of tissues, and microscopic anatomy. General anatomy is the most inclusive. Histology is only a small part of general anatomy, which also includes general morphology, the study of the form of the animal body, especially in connection with the vertebrata, as well as the general physical properties of the component parts of the human and animal body. Chemical considerations, of course, come in also. Microscopic anatomy is, on the contrary, an artificially created division which practical necessity has permitted to remain. It belongs to descriptive as well as to general anatomy, and has no sharp limits from descriptive anatomy as far as this can be determined by observation with the naked eye. With the same justification one might speak of a maceration anatomy, of a staining anatomy, of a dissection anatomy of a serial section anatomy. By the retention of the term microscopic anatomy we only satisfy a practical need. It must be clear to us that it remains description, whether the anatomy of the external form and relationships, for instance, of the human liver is depicted, and the form, color, and limits of the lobes is described, or whether the construction of these lobes from special liver cells, as the essential part and from a connective tissue framework with blood and lymph vessels, nerves and fine bile-ducts, is demonstrated and the details of their relations described.

This, in my opinion, is the way in which the realm and position of human anatomy in the plan of science must be considered.

In conformance with the task set before us, we must now determine to what causes and motives the development of human anatomy is due, and which sciences have assisted in its development.

We may divide the causes and motives into immediate and mediate. As far as we can tell, it was the needs of medicine and of the treatment of the sick which, in the most ancient times, gave origin to the investigation of the human body. I do not consider here the knowledge of the external form, which the simple observation and examination of the naked body and the necessity of naming the individual parts must give. Animal sacrifice and divination from sacrifices, still more human sacrifice and cannibalism, as well as the examination of large wounds and the natural attempt to bind them up, in order to stop hemorrhage and to replace dislocated limbs, as well as the occurrences during delivery and in many other connections, gave man from his first appearance on the earth an opportunity to attain anatomic knowledge. We find it among the primitive people of to-day, to the extent to which a people without script can attain. The oldest anatomic and medical writings which have come down to us show, already, a mass of facts obtained in the above way, which was perhaps greater than those in any other realm of biology at that time.

Knowledge developed more rapidly with the awakening of scientific medicine. At first it was naturally the requirements of practice, particularly those of surgery and obstetrics, which were the cause of development. The requirements of internal medicine were not felt until later. Much later, but with so much the greater energy, physiology, zoölogy, comparative anatomy, and human pathologic anatomy showed their effect. The last, as well as human physiology, is inconceivable without an accurate knowledge of human anatomy. Zoölogy, comparative anatomy, and embryology are not absolutely necessary to human anatomy, but none of these sciences can fully reach its goal without a knowledge of the most highly developed creation, man.

State medicine felt the need of caring for anatomy among the latest of the branches of medical instruction, but finally furthered anatomic study. At the same time jurisprudence comes into relation with anatomy, with animal as well as human.

In all of this connection, excepting that of jurisprudence, the biologic character which all have in common played a part. But even the purely mental sciences, especially philosophy, and in this, above all, psychology and the theory of perception, as well as the history and beginnings of philosophy, required a study of anatomy for their further development. The relations of the latter to psychology and the theory of perception, as well as to other branches of philosophy, first became striking when we began to penetrate more deeply into the finer anatomy of the brain. Here, in spite of books so numerous that one might fill libraries with them, we still stand in the first stage of our knowledge. The anatomy of the brain is of little more use to philosophers than was the Galenic anatomy to the surgeons of that time. Philosophy will thus remain one of the factors which continually stimulate more detailed anatomic studies. We shall return to this later.

Manifold are the facts concerning human anatomy which are found in history and tradition. In the first place, the history of human anatomy is an important part of general history, especially of the history of education. To determine the history of anatomy requires a considerable knowledge of the subject. Illustrations of anatomic objects occur frequently among prehistoric remains. I will recall only votive tablets and relics. With an accurate knowledge of anatomy, many facts in the history can be rightly determined. The method introduced and developed by Welcker, His, and Kollmann, of reconstructing the head by placing skin and hair over the skull bone, can be of importance in the determination of the identity of a personality. Although we are now only at the beginning, I am convinced that we may expect much of value from this method.

The reconstruction of the head has, also, a relation to one of the most important non-medical contributors to anatomy, the fine arts. Since early times its requirements have given an impulse to the study of anatomy, especially to that of the external form and the anatomy of bodies in motion. We may, indeed, say that it was the artists who first developed and furthered the study of this branch of anatomy. I need only recall Leonardo da Vinci, Michael Angelo, Raphael Sanzio, and Albrecht Dürer. To this point also we shall return.

Finally, we may say, according to the proverb, "Homo sum, humani nihil a me alienum puto," that everything connected with man and with humanity requires a knowledge of the construction of the human body. We need not be surprised, therefore, if advances in the study of anatomy come from unforeseen and unexpected directions. I shall only mention here the great realm of sociology and personal hygiene.

Although these are the principal factors which have required a study of human anatomy, and which in the future will impel a progressive development and increase in the knowledge of the same, there is one factor which must not be left out of consideration, which is and will remain active in the development of all sciences, as well as of human anatomy. This is the great advance in the general condition of scientific and public life, as well as in the condition of the masses. Such advances may require a long preparation, but in a short period great advances and discoveries will occur, astonishing the people themselves. Thus, fortunate political conditions, political revolutions, and social changes, even fortunate wars, whose result is a long time of peace, may mean the beginning of a new period, as well for the conqueror as for the conquered, accompanied by rapid development in all branches. All these things act as yeast upon the intellectual labors of a people. Can it be a mere coincidence that the first improvement of medical knowledge by the Hippocratic school occurred at the time of Pericles, that the Galenical school followed soon after the bloody time of the Roman emperors, that previously the development of anatomy in a high degree occurred in the short and bloody period of the Ptolemies, or finally, that the almost phenomenal blossoming of anatomy at the time of Vesalius, Eustachius, and Fallopius followed soon after the beginning of the Renaissance, the invention of printing, and the discovery of America? A wonderful period this was at the beginning of the sixteenth century!

Philosophy, the mother and starting-point of all sciences, in which they all come together, assisted materially in its development, not only because it placed new problems before anatomy, but because its recent conceptions and systems have affected the progress of anatomy and that of related sciences, to a degree hardly suspected by those who have accepted its ideas. The philosophy of Cartesius and the application of the inductive method by Francis Bacon, Bacon of Verulam, were, of course, not without an influence upon all natural sciences, as well as on the development of anatomic teaching.

But we should appear thankless, if we did not mention the valuable assistance which influential and sagacious men, be they rulers and statesmen, be they wealthy burghers, have given to the cause of anatomy. The Ptolemies, Medicis, many of the popes of the sixteenth century, the Hohenstaufens, Frederick II, and others have assisted by laws and regulations in the development of anatomy, at a time which was most difficult and unfavorable for the same. In this country, in which all sciences are advancing with an unexampled energy, a steadily increasing number of large-hearted citizens consider it their greatest honor to use their hard-earned wealth in the service of science.

Human anatomy has also received valuable aid from the founding of universities and other scientific institutions. If the problems may be mentioned which anatomy has still to solve, it will be shown that special grants for the same are among the most worthy objects for wealthy donations.

Our science, as all others, may hope for considerable advance from the coöperation of the academies and learned societies of the whole world, which has been brought about at the end of the century by the "Association of Academies." The first problem which was taken up by the Academies this year, the advancement of the study of the brain, is in large part anatomic. I cannot neglect referring in this place to the name of William His, who studied this problem with all his mighty energy until his death, which occurred May 1 of this year, —praising him, and at the same time regretting that he could not survive the taking-up of this task by the Academies.

In addition to the medical sciences, which we have already mentioned among the mediate influences, other natural sciences have had an immediate influence upon the development of anatomy. If medical sciences must be mentioned here again, this is justified by the fact that surgery, internal medicine, obstetrics, and the many modern specialties, have had an immediate influence upon anatomy, by their careful investigations on the living and the comparison of healthy with diseased organs. They have discovered many new facts and shown others in the proper light, but this need not be gone into in detail here.

In addition to the medical branches, human anatomy must be especially indebted to botany and zoölogy; above all, however, to embryology and comparative anatomy. Botany helped especially in the first completion of general anatomy, above all, the study of the cells and tissues, and has advanced in this direction considerably farther than human and comparative anatomy. The cells themselves were first discovered by botanists, but this is easily understood, because the botanical objects are generally much easier to prepare, and especially to examine in the fresh state, than those of zoölogy and human anatomy.

Besides these, physics in all its branches, chemistry, and mathematics, have given much aid to the anatomists and will continue to do so.

It is, in the first instance, the estimation of mass, number, and weight whose improvement and refinement have always exercised a beneficial influence on anatomy. I shall mention here only the balances, the pelvimeter, the measuring-scale, the measuring-cylinder, the micrometer, the kinds of delicate counting-apparatus, the manometer and thermometer, and the apparatus for the determination of capillarity. We may also mention here the principal mechanical instruments of anatomists, knives, scissors, sounds, tubes, and syringes.

Especially interesting is the history of the microtome, which was first made use of by the before-mentioned anatomist of Leipzig, William His. In this case mechanics received a great furthering from anatomy, before which the problem of making an uninterrupted series of extremely thin sections of the most various objects was placed.

We could hardly believe, unless we were familiar with the subject, what difficulties were here to be overcome, and how much genius was required in the performance of this task, and we are still working at the problem.

When we compare the old anatomical apparatus of Leyser (or Lyser), which is described in his *Culter Anatomicus* with a complete anatomic armament of the present time, we see at a glance the great progress which has been made in this elementary part of technique. The great influence of the above-mentioned sciences is also shown in the material which we use to-day, improved steel, nickel-plated instruments, etc.

This influence is even more marked in the realm of optics. If we require any proof of the fact that one science can be helped by another, we have only to mention the relations of optics to human anatomy, and, of course, its relation to the other natural sciences.

No other agent has done more to illumine the obscure subject of the human body than has light, from the simplest arrangements for good illumination, by the correct disposition of windows in the dissecting-room, to the ultra-microscope and radioscopy or "Röntgography." Artificial illumination has made such extraordinary advances in our time that, especially with electric lighting, we can concentrate the light upon any given point and limit it as we will. Then we have the various mirrors, the vaginal speculum, which was known to the physicians of ancient Greece and Rome, the laryngeal mirror, whose fifty-year jubilee we celebrate to-day, the rhino-, pharyngo-, and œsophagoscopes, the otoscope, the cystoscope, and above all Helmholtz's brilliant discovery, the ophthalmoscope, whose latest stereoscopic modification by Dr. Thorner may be seen here in the German "Department of Education." All these discoveries have, in addition to their practical importance, been of the greatest service in the study of human anatomy, especially that of the living, and will still continue to be.

The electric light permits, by its endless adaptability, a large number of additional applications, especially for the illumination of body cavities and hollow organs. I will recall only the transillumination of the accessory sinuses of the nose.

From lenses and eyeglasses, among which are the dissection eyeglasses of Brücke, we pass to the simple and later to the compound microscope, one of the most important inventions which has ever been made or will ever be. How great the progress is which results every year in this special realm, is also shown here by the exhibition of the noted firm of Zeiss in Jena. Every step forward which is made here is of great benefit to human anatomy.

For anatomic study and the demonstration of new facts, we may mention the drawing apparatus, the projection apparatus, the episcope, and epidiascope, and above all, photography, whose future development we cannot yet foretell. With this discovery, France, which opened the way and has always led in the investigation of light, has made an advance which cannot be too highly valued.

As, in the starry heavens, the photographic plate shows us worlds which could have been recognized in no other way, so also the same plates show us finer details in the structure of the bodily tissues, which were only incompletely seen before. It fixes our eyes upon them, makes possible comparative observations, and makes much certain which otherwise would have remained doubtful.

Radioscopy stands above all others in its great value for descriptive and topographic anatomy. This it is which, in the truest sense of the word, has illumined the obscurity of the human body, and, in connection with photography, has been one of the most important advances, not only in anatomy, but in general medicine. Only a few years have passed since Röntgen, then living at Würzburg, made his overwhelming discovery, and the World's Fair Exhibit at St. Louis convinces us to-day of the extraordinary importance which it has won for medicine.

Physics and chemistry meet in the technique of injections, which are so important for the advancement of anatomy. The manufacture of a suitable apparatus, the syringe, in which also the air-pump plays a rôle, falls to mechanics, as do the thermometer and manometer, and, on the other hand, the production of a suitable material is aided by chemical studies. Since Ruysch of Holland, who was the first worker in this field, and his famous countryman, Swammerdam, Lieberkühn in Berlin, Hyrtl in Vienna, Thiersch, the surgeon of Leipzig, the optician Schöbl in Prague, the anatomist Teichmann in Krakau, Sappey in Paris, Taguchi in Tokio, Dalla Rosa in Vienna, and Gerota, who was at that time assistant at the Berlin Anatomic Institute, and is now professor at the University of Bukarest, have done great service in this field; those since Teichmann especially with the difficult injection of the lymph-vessels.

Teichmann prepared an injection-mass which is still the best for the rougher lymph- and blood-vessel injections. Sappey developed the mercury injection, which had been used by the older anatomists, Monro, Mascagni, Cruikshank, and Fohmann. Taguchi and Dalla Rosa used Japanese and Chinese India-ink, which had previously been used by von Recklinghausen for the injection of large and small lymph-vessels. Gerota's injection-mass, devised a few years ago, and the syringe of his own construction, denote a marked advance in the technique of the injection of the smaller lymph-vessels, which has already made possible important advances in human anatomy.

These injections with soft masses were followed recently, in Berlin, by the injection of fluid metal masses, devised by Wood and Rose, which after hardening permit no more change of shape in the injected vessels or canals, and thus are of especial service in topographical anatomy. The method is also of value because Röntgen pictures of the vessels injected with metal can be taken, and thus we may determine their position without their being distended or stretched. Recently quicksilver injections, on account of their simpler technique, have been used a great deal for the taking of radiographs, but displacement and distortion are not excluded. Further study will determine what is best in each case.

The injections of the blood-vessels of human bones recently carried out by Lexer of Berlin, with a special technique, show that important advances may be daily expected, as these injections have shown certain points which were hitherto unknown to anatomy. Radiographs of the same may be seen here in the German "Department of Education."

A procedure which is closely related to injection is corrosion. I believe that corrosion following injections of metal was first carried out by Bidloo. Hyrtl was recognized as the master of this method, but in the hands of F. E. Schulze, Merkel, Schiefferdecker, Zondeck, and others, striking results have been obtained in the anatomy of the viscera, especially of the lungs and kidneys.

The various procedures which are proposed to conserve the material of human anatomy are more allied to chemistry. Here we may consider the preparation of bodies for dissection, the conservation of separate organs, the special methods of preparation, and finally those for exhibition purposes in museums. Thus we may here distinguish between a preparatory technique, a special technique, and a museum technique. We may add that these are different for macroscopic and microscopic anatomy. I cannot stop to mention all the points in which anatomy must be grateful to physics and chemistry in this connection, but shall only mention those which have been recently developed. For the conservation of objects for investigation the method of freezing has been used, especially in America. France, and especially Russia, have made us familiar with the technique of frozen sections, which was raised to its highest point by W. Braune.

Recently in America simple hardening in strong formalin solution has been used instead of freezing. I have seen here, with Professor Potter of the St. Louis University, especially fine formalin specimens and sections.

The use of chemical methods has advanced us materially in the art of macerating and bleaching bones. I will again recall in this connection the anatomist of Krakau, Ludwig Teichmann, my teacher in anatomy. The fibrillation procedure of Jacob Stilling of Strassburg, which promises good results in the preparation of brains, nerves, and muscles, also rests upon a chemical reaction.

The technique of microscopic anatomy may also be considered as related to chemistry. We no longer stand upon the purely empiric basis which has existed since the introduction of carmine into the technique of staining by J. Gerlach of Erlangen, when we wish to determine the use of a new stain. Three procedures must be mentioned as especially valuable, the corrosion method of Carl Weigert of Frankfurt-on-the-Main, whose early death was deplored by all anatomists of this land, the staining *in vivo* of Ehrlich, who is also known all over America as an investigator of the first rank, and the method of Dr. Kaiserling, who assisted the German universities in arranging their exhibition here a few months ago, the method of preserving anatomic preparations so that they retain their natural colors for a period of time hitherto not thought possible. The exhibition of the Berlin Pathologic Institute will give everybody an opportunity of convincing themselves of the superiority of this method for normal, as well as pathologic, anatomy.

I can only refer in passing to the procedure of Golgi for the microscopic study of the central nervous system, and its recent improvement by S. Ramon y Cajal of Madrid, the method of Coccius, His, and von Recklinghausen, of impregnation with silver, that of J. Cohnheim, of impregnation with gold, and the osmic acid fixation method of Max Schultze. I may also mention that an encyclopedia of the technique of micro-anatomic methods has recently appeared in Berlin under the editorship of Rudolph Krause, which occupies a large quarto volume, and shows adequately how great an advance has been brought about in anatomic methods by the study of chemistry.

Of the art methods, that of taking casts is especially to be mentioned, which has been adapted to scientific purposes by W. His and by Born's method of modeling with wax plates. These not only serve for the obtaining of specimens for investigation, but also to clear up obscure topographical relationships, especially in embryonal anatomy and the form of certain cavities. A glance at the section of this exhibition where this is displayed will show what a great importance and high development the technique of taking casts has reached.

It may be mentioned that the relation of the fine arts to human anatomy was developed, to a high degree, many centuries ago. Illustrations for purposes of instruction were prepared by Henri de Mondeville (about 1300), and we find some in the book of Berengarius da Carpi about 1500. The recent advance in anatomic illustrations, in books, and in atlases, is shown by all the journals, archives, and periodicals connected with the subject. It is also seen in our text-books, which have been prepared in great number in the United States, of which I will only mention the excellent topographical anatomy of Deaver, the classic work of W. Braune and Sappey on the same subject, and on the anatomy of the lymph-vessels, the recent atlases of

Toldt, Spalteholz, Brösike, Sobotta, O. Schultze, and above all, the anatomy of the human embryo by W. His. Some of these books, which are well adapted to show the influence of the recent improvement in the technique of illustrating on anatomic teaching, may be seen in the German "Department of Education."

Finally, I will merely touch upon the marked influence which the founding and continuing of special archives and journals and regular yearly reviews and yearly compilations have had upon anatomy, as well as upon all other sciences. I may also mention the societies for the study of anatomy (since 1886) and the *International Cyclopædia of Literature* recently prepared by the London Royal Society. Anatomy must also be grateful to philology, as this has made possible the systematization of its extremely complicated nomenclature. The start in this direction was made in Germany at the suggestion of W. His. We may hope that in the same way an anatomic language which will be adapted to all people will develop and retain the interest of succeeding generations in scientific unity. I am of the opinion that this will only be possible by the historic method.

When we pass to the second part of our subject, the consideration of the influence and improvement which has been exercised by human anatomy upon other branches of art and science, we may dispose of it much more briefly, because the influence is generally reciprocal. We shall enumerate the branches concerned, as far as may appear desirable, and give examples here and there. It is not necessary to insist upon the great importance of anatomy to the other medical sciences. Following a noted saying, we may state "Anatomia est fundamentum medicinae." Before Richard Lower had discovered the course of the vagus nerve to the heart, there could be no thought of a physiology of the cardiac action, and Marcello Malpighi's discovery of the capillary blood-vessels set the keystone to Harvey's doctrine of the circulation of the blood. We know how important the determination of normal anatomic facts is for pathologic anatomy, and it is not in vain that our pathologic anatomists constantly turn to the study of normal anatomy. Men like Morgani and Rudolph Virchow, Cohnheim, Cornil, Marchand, Orth, von Recklinghausen, Carl Weigert, and others have clearly understood the importance of this close connection.

The problem of embryology could only be definitely determined when Karl Ernst von Baer, in the year 1817, discovered the mammalian ovum. The detailed investigations of human anatomy, which have been performed more carefully than those of any other animal, are of the greatest importance for comparative anatomy and zoology.

We may also see how more accurate anatomic knowledge has been of use to practical medicine, in the physical methods of investigation in internal medicine, and in many other ways. How this has helped the latter may be seen by a reference to lumbar puncture, introduced by Quincke, which is constantly becoming more important, and which could only be performed after the detailed anatomic investigations of Axel Key and Gustav Retzius. This method has also brought about a long series of anatomic studies. That we may conclude with a more general example, let us recall what a mighty and beneficial influence on the development of internal medicine was exercised by Hermann Boerhaave, whose *Institutiones Medicae* and *Aphorismi de Cognoscendis et Curandis Morbis* rest entirely on an anatomic basis. We may also recall how great an influence was exercised by the memorable *Anatomie Générale* of François Xavier Bichat. Was not the cell-doctrine necessary, before a scientific bacteriology could develop? How carefully every obstetrician and gynecologist must study the human pelvis, and every new discovery which is made in this branch of human anatomy is of use in practice. The history of the last few years shows that much is yet to be learned. What can I say of surgery, in which anatomy must constantly watch over the course of the knife?

The great influence of anatomy on practical medicine is, however, shown most markedly in special branches, laryngology, rhinology, otology, neurology, urology, etc. When a physician wishes to devote himself to any of these branches, he first studies carefully the anatomy of the particular part. If he has forgotten this, he is forced to review it carefully unless he wishes to become a charlatan. The anatomists can instruct him on this point, and it is not necessary for me to speak more at length about it, in this country in which special branches are so strongly developed.

We need not prove that human anatomy forms an indispensable basis for anthropology, ethnology, and sociology. We need only recall the names of Blumenbach, R. Virchow, and Anders and Gustav Retzius, father and son.

Further study and advance in the knowledge of anatomy is also important for philosophy, especially for psychology. This stands to reason. The investigation of the brain is the task of human anatomy. The organ of thought must be investigated to its smallest details, and we may state without fear of contradiction that philosophic sciences will burst into renewed bloom, when anatomy and physiology have cleared up the dark and intricate labyrinth of the brain. Much that can now only be reached with effort, and is then hardly clear, will become comprehensible.

And now, last, not least, the fine arts. The representation of men, be it as a true and characteristic imitation, as a portrait, be it in historic paintings, in ideals, in caricatures, whether with the brush and pencil or with the knife and chisel, will always be the principal task of the fine arts and demand its greatest powers. To give a picture exact in the smallest details, I might say a photographic representation of the human figure, is not the aim of art. It should much more give what is characteristic in the expression, in a portrait, as the position of the limb and the attitude of the body should stand in relation to the expression in painting, and, I may say, give the point to caricature. In order to illustrate the last point, tell the same joke to two different persons; one breaks forth spontaneously into hearty laughter, while the other laughs only in order not to seem discourteous.

I can give no better example of what photography may do for us, than the exhibition of persons walking, which are often shown in our illustrated journals. The photograph has exactly shown the phase of the step, at the moment of the exposure, and yet this reproduction is ugly and even ridiculous. The step as a whole is composed of a coördinated series of little motions, which we may analyze by instantaneous photography. When we arrange these "phase pictures" close to one another, by a special apparatus, the kinematograph, the natural movement of walking again appears. The artist must understand this. He must represent motions, in his figures, at the most characteristic time. Then their effect is natural, and they attract us. I see, in the fulfillment of this task, the anatomic side of the fine arts; and here anatomy has been of the greatest service to art, and with the development of methods will become still more so. Thus the artist must study human, and in certain cases animal, anatomy, as this gives a firm basis for the further study of the living body, in rest and in motion. From the naked figure we shall then pass to the clothed, and study the changes which are made in the position of the standing and moving figure by restricting garments. Thus are made the magnificent draped figures, in statues and paintings, which so please and surprise us. The observation and close imitation of nature, combined with idealistic modification of the same, is what we wonder at in masterpieces. Although the head of the Venus of Milo is treated somewhat conventionally, we cannot deny that the rest of the body lives, and we expect, every moment, the marble breast to stir with life. It is this, also, which attracts us to the masterpiece of Velasquez in Prado, "Las Lancas," and which causes us to gaze with wonder and sympathy at the motion and expression of the two principal figures. This is also shown in the portraits of this painter, perhaps the most noted of all artists, and also in the portraits of Holbein, Dürer, Raphael, and Rembrandt.

We find the same truth and comprehension of nature in the small and quiet figures of Meissonier and Millet, and we find it again in the marble statues of Hildebrand and Schaper, whose statue of Goethe, in the Berlin Zoölogical Garden, appears to me to be the model of an idealized draped figure in a position of rest. It is not possible to reach the greatest perfection without careful anatomic studies, either on the dead or on the living. I am well aware that there have been good painters who have bothered little about anatomy; it is not anatomy alone which enables the artist to perform great works; but perhaps every one of those masters who has not been well trained in anatomy would have done better with a good anatomic knowledge. That which belongs to the artist, as such, can only be strengthened and refined by a careful study of anatomy. The before-mentioned great artists of the fifteenth century realized this perfectly, as is shown by the numerous anatomic studies which they have left. Fra Bartolommeo worked in the same way.

Thus we see that human anatomy receives much from her sister sciences and from the arts, and gives much to them, and what she gives is greater and more valuable than what she receives. This is because she is the basic science of all biology, because she has made the most highly organized being the subject of her studies. Besides, she has the advantage that she may be assisted by observation of one's self, as can no other branch of biology. We shall only comprehend the mechanism of the living body when our anatomy of the human central nervous system is further developed. Here we are still, as I have already mentioned, only at the beginning of our knowledge. Let us hope that interest in our investigations and methods will receive greater diffusion by the example of the founding of the academies of the world. Let us hope that the horror of the material of anatomists will disappear more and more from all classes of humanity, especially from the circle of the educated. We must attempt to reach the point where all assist with the good work. *Sapienti sat.*

THE PROBLEMS IN HUMAN ANATOMY

BY HENRY HERBERT DONALDSON

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For the solution of the problems presented to him, the anatomist is by no means limited in his technique to the scalpel or the microscope, but justly claims the right to use every aid to research which other departments of science are able to furnish. His position, therefore, in the scientific field is determined by the standpoint which he occupies and from which he regards animal structures, rather than by any special means and methods employed for their study.

By common consent anatomical material includes not only structures which may be easily dissected and studied with the unaided eye, but also those which tax the best powers of the microscope for their solution. But even within such wide limits the material that ordinarily comes to hand leaves much to be desired, and in elucidating this or that feature in the structures under examination, it is often found necessary to modify the physiological conditions under which these structures have been working, in the hopes that their appearance may be altered thereby, and so be more readily understood.

Taken in a broad way, this is the reason why the data of pathology and experimental morphology are so important for the development of anatomical thought, helping as they do in the solution of the problems connected with the finer structure of the animal body, just as embryology and teratology illuminate the gross morphological relations in the adult.

I am quite aware that in making the foregoing statements I have suggested more modes of investigation than are at present used in connection with man. But the anatomy of the human body in adult life forms in itself so limited a field that no investigator can possibly confine himself to this portion alone, and there is every reason for here treating the subject in the larger way. As we see from the history of human anatomy, it was brought into the medical curriculum in response to the demands both of physiology and surgery, but gradually became most closely associated with the latter. For a long time its relative significance as a medical discipline was very great, because it represented the only real laboratory work which appeared in the training of the medical student. Indeed, a generation ago the exactness of anatomical methods was so lauded in comparison with the methods then commonly used in medicine, that anatomists came to scoff at the vagueness of their colleagues, while to-day, if we may be persuaded by some of our physiological friends, they have remained only to prey on the time of students who might be better employed. Although such a thrust may be readily parried, it is, nevertheless, necessary to admit that times are changed, and that as a laboratory exercise human anatomy is to-day outranked by several of the subjects in which the laboratory work permits a more precise formulation of problems and their more rapid and definite solution. However, it still retains, rightly enough, much of its former eminence.

Among the problems in human anatomy, there is, perhaps, none more important than the way in which it is to be presented to the five young gentlemen ranged around a subject in the somewhat trying atmosphere of the dissecting-room. Just what they may be expected to learn from such an experience would require some time to state. Certain it is that these beginning anatomists are almost all of them intending to become physicians, and some of them to become surgeons, and to this end they are building up a picture of the human body which will be useful to them in their profession. They are doing this by the aid of the best pedagogical means at their command, namely, the reinforcement of the ocular impressions by the contact and muscular sensations that come from the actual performance of the dissection itself. If previously they have had some experience in the dissection of the lower mammals, they will note at once the differences shown in the case of man, and if their embryology is at their command, it will be easy for them on suggestion or on their own initiative to appreciate how some of the peculiar relations between parts of the human body have been developed. Beyond this the information obtained is of the same order as that of the vocabulary of a language. The student gets a certain number of discrete pictures of the different parts of the body more or less clearly impressed upon his mind, and when he has occasion later to deal with these same parts, he has the advantage of finding himself in the presence of familiar structures. How far in this first experience the special groups of facts which are sometimes set apart under the head of surgical anatomy should be introduced, is a more or less open question. The present weight of opinion demands that they should still be kept by themselves. Nevertheless, while the anatomical experience of the average medical student should rest on a broad scientific background, he should at the same time have a distinct appreciation of the eminently practical value of the information he is expected to acquire.

The question at once arises how the monotony of long-continued dissection can be relieved, and the student maintained in a condition of sufficient receptivity to make the work really worth while; for the acquisition of vocabularies has never been counted as one of the greater pleasures of life. There are several legitimate devices: in the first place, if it is possible, for the student to have near at hand a microscope which may now and then be used for the examination of the different tissues as they appear in the cadaver. This cross-reference between the gross and microscopic appearance will serve to bring into close connection with one another two classes of facts which are often separated to their disadvantage, and to revive the histological pictures which should be incorporated in gross structures, but which in most cases remain forever apart from them. On the other hand, a search for anomalies or variations serves to give both a reality and purposefulness to the work and to make a student feel that in return for the large amount of time necessarily required for his anatomical training, he is, in some small measure at least, contributing to the science. It is unavoidable, this expenditure of time, and absolutely necessary that the student should do these things with his own hands, in order to obtain the three-dimensional impression of the structure with which he deals.

In this connection just a word as to the way in which the beginner may be aided in the comprehension of his work. The excellent diagrams and pictures which are now used to illustrate the b st anatomical text-books carry us as far as that means of assistance can probably go. Pedagogical experience points strongly, however, to the superior value of the three-dimensional model, and although such models are more difficult to collect, harder to care for, and require more space and caution in their use, they are so far superior to any other device, except an illustrative dissection itself, that the collection of them in connection with anatomical work becomes a moral obligation.

If we turn now to the wider uses which may be made of anatomical material as it usually appears in the dissecting-room, we find that a number of directors of laboratories have been utilizing this material for the accumulation of data in such a form that it may be later treated by statistical methods. Thus they have weighed and measured in different ways various parts of the cadaver, and in some cases determined the correlations between the organs or parts examined. It cannot be too strongly emphasized that the results thus obtained are to be used only with the full appreciation of the fact that the material ordinarily available for examination in the dissecting-room belongs in all countries to a social group which contains the highest percentage of poorly developed and atypical individuals. The conclusions, therefore, that can be drawn from the investigations of this material must always be weighted by its peculiar nature. To illustrate what is here meant by the peculiar character of this material, we may take as an instance the bearing of the results obtained from material of this sort on the problem of the brain-weight in the community at large. It must be admitted that the figures which we have at our command for this measurement are, with the exception of one short list, derived from the study of individuals belonging to the least fortunate class in the community, and it is not fair, therefore, to carry over these data and apply them directly to the average citizen who is of the normal type and moderately successful in the general struggle for existence. From what has been said, it is plain that much of the work now being carried on in the dissecting-room comes very close to the lines which have been followed for years by the physical anthropologists; yet, because these have for the most part concerned themselves with the study of the skeleton, have limited their comparisons to the various races of men, and have developed no interest in surgery, they have for a long time stood apart, and only recently joined forces with the professional anatomists. This step has certainly been to the advantage of anatomy, and as one result of it, anatomical material not previously utilized will now be treated by statistical methods. But all the work to which reference has here been made is on the body after death. So manifest are the disadvantages arising from the conditions which are thus imposed that the necessity is felt on all sides of extending our observation as far as possible to the living individual. As an example of such an extension, we have the determination of the cranial capacity and brain-weight in the living subject which has resulted from the labor of Karl Pearson and his collaborators.[1] The methods which have been employed for this purpose are capable of giving as accurate results as are ordinarily obtained from post-mortem examinations, and, moreover, have the advantage of being applicable at any time to any group in the community which it is desired to investigate.

To redetermine, as far as possible, from studies on the living, all the relations which have been made out post-mortem, becomes a very immediate and important line of work.

But even under the general limitations which apply to the dissecting-room material, it is desirable to refine our knowledge of

[1] Pearson and collaborators, *Phil. Transactions* of the Royal Society, 1901.

the human body by classifying the subjects according to race, and thereby bringing into relief the slight anatomical differences that exist between the well-marked races of Europe and the races of other parts of the world. The history of anatomical differences due to sex lacks several chapters, and it is possible also to show the modifications of structure which come from the lifelong pursuit of certain handicrafts which call for peculiar positions of the body or for the unusual exercise of certain muscles; as, for example, the anatomy of a shoemaker.[1]

Such results as the one last mentioned have a direct bearing on the modifications of the human form which may be introduced by peculiarities of daily life and work, and bring anatomy into connection with the problems of sociology; while, on the other hand, both lines of work are contributory to the broader questions of zoölogical relationship and susceptibility to modification.

Yet when we have gained all the information which the scalpel can give, there still remains the whole field of finer anatomy, the extent of which it is so difficult to appreciate.

While recognizing that the human body may be regarded as a composite, formed by the fitting together of the series of systems, and while, in some instances, we have a more or less accurate notion of the way such a system appears, — as, for instance, in the case of the skeleton, — yet a much better understanding of the relation of the soft parts would follow an attempt to extend this method of presentation, and to construct phantoms of the body in the terms of its several systems in some way which would show us the system in question as an opaque structure in a body otherwise transparent. This is, of course, the final aim of the various corrosion methods, or those which depend on injection or differential coloration of structures which may be viewed in three dimensions.

When the vascular, lymphatic, nervous, and glandular systems can be thus exhibited for the entire body, or for the larger divisions of it, it will be possible to see the human form transparently, and to see it whole; a feat difficult to accomplish, but worthy of earnest endeavor. The development of such phantoms should serve to make more impressive the familiar fact that in many organs and systems the total structure is built up by a more or less simple repetition of unit complexes, as, for example, the liver by the hepatic lobule, the bones by Haversian systems, and the spinal cord by the neural segments.

If we pass now from the consideration of the systems of tissues to that of their structural elements, we enter the domain of his-

[1] Lane, W. A., *Journal of Anatomy and Physiology*, vols. XXI and XXII, 1887 and 1888.

tology and cytology. Starting with the differentiation of the tissues by means of empirical staining methods, investigators have gradually come to appreciate the chemical processes which underlie the various color reactions, and as we know now, there already exist methods for determining in the tissues several of the chemical elements, such as iron, phosphorus, etc., to say nothing of the more or less satisfactory identification of complex organic bodies by means of definite reactions. This being the case, it is possible to imagine representations of the body built up on the basis of these microchemical reactions, representations which would show it in the terms of iron or in the terms of phosphorus, thus yielding us an image which might be compared with that obtained by aid of the spectroscope when the picture of the object is taken by means of one out of the several wave-lengths of light which come from it.

The contemplation of the multitudinous opportunities for investigation and comparison which appear within this field lead us to pause and inquire what is properly the purpose of all this anatomical work; for without a strong guiding idea we are liable to repeat the errors of earlier generations, and merely accumulate observations, the bearing of which is so remote from the actual course of scientific progress that the investigations are mainly useful as a mental exercise for the individuals who conduct them. Anatomical results begin to have a real meaning only when correlated with physiology, and when we learn that a tissue with a certain structure is capable of performing given functions, we feel that we are really bringing our anatomy into touch with the life-processes. It is to aid in the accomplishment of this end that men devote their lives to anatomical work. With the variation that we find everywhere in organic structures, it should be and is possible to discover by comparison what variations in the structure of a tissue or a cell are accompanied by the best physiological responses. It is along this line that we must necessarily work in order to reach human life, either through medical practice or other avenues of approach, for in the end the object and purpose of all science is to ameliorate the unfavorable conditions which surround man, and in turn to produce a human individual more capable of resistance to disturbing influences, and better suited for the enjoyment of the world in which he lives.

Considering anatomical work with this thought in mind, the problems which it presents can be grouped according to their relative value and importance. The approach may be made from two sides. On the one hand it is, for example, extremely worth while to direct years of labor to the determination of the finer structure of living substance, because the more closely we approximate to a correct view of that structure, the more readily will our anatomy and physiology run together, and the clearer will be the conception of the sort of structure which it will be most desirable to increase for the attainment of our final purpose. On the other hand, if we follow the path from the grosser to the finer anatomy, we are led to inquire whether there is any one part or system of the human body which at the present moment is specially worthy of attention. When we say that the nervous system is such a part, I think that even those who are not engaged in the study of it will admit that there are some grounds for the statement. The peculiar feature which sets the nervous system apart is the fact that its enlargement, both in the animal series and during the development of the individual, is in a very special way accompanied by changes in its physiological and psychological reactions. To be sure, we think of it as built up fundamentally by the union of a series of segments, but the relationship established between these segments becomes ultimately so much more important than the constituent units that in the end we find ourselves working with a single system of enormous complexity, rather than a series of discrete units; a state of affairs which is not paralleled in any other tissue. In addition to this, the nervous system as a whole is *par excellence* the master system of the body, and as such, the reactions of the organism are very largely an expression of its complexity. Indeed, within the different classes of vertebrates, the various species may be regarded as compound bodies composed of four fundamental tissues, and a species could well be defined by the quantitative relations found to exist between the nervous, muscular, connective, and epithelial constituents. Working from this standpoint, Dubois,[1] the Dutch anatomist, stimulated by the work of Snell,[2] has brought forward evidence for the view that when, within the same order, several species of mammals similar in form, but differing in size, are compared with one another, the weight of the brain is found to be closely correlated with the extension of the body surface, and by inference with the development of the afferent system of neurones. This view would seem to imply that in these cases there is the same density of innervation of each unit-area of skin; but the correctness of this inference can only be determined by the careful numerical study of the afferent system of the animals compared. It will appear, however, that under the conditions imposed the relative weight of the brain depends upon the fact that each unit-area of skin, represented by the nerves which supply it, calls for a correlated addition of elements to the central system, and thus the increase in one part is followed by a corresponding increase in the other. When, however, the large and small individuals within the same species

[1] Dubois, *Archiv für Anthropologie*, 1898.
[2] Snell, *Archiv für Psychiatrie und Nervenkrankheiten*, 1892.

are compared, it is found that the increase in the brain-weight follows quite another law, and that in this latter case it is relatively much less marked than in the former. This result at once suggests that the mechanism of the increase is dissimilar in the two cases. For the solution of the problems that are raised by such investigations as those just cited, we need to employ quantitative methods, and on this topic a word is here in place.

Microscopic anatomy and histology, like all the sciences, have passed through a series of phases which are as necessarily a part of their history as birth, growth, and maturity are a part of the life-history of a mammal. The microscope in its early days enabled Schwann to propound the fruitful theory that the tissues were composed of cells. A preliminary survey showed that these cells were different in their form and arrangement in the different parts of the body, and a still more careful examination with the aid of various dyes or solutions altering the tissues in a differential way gave the basis for yet finer distinctions. This phase in the development of the science, however, may be fairly compared with qualitative work in chemistry, where the object is to determine how many different substances are presented in the sample examined. Naturally, the next step is the introduction of quantitative methods, and we are, therefore, now using the methods of weighing, measuring, and counting for the purpose of rendering our notions more precise, and thereby facilitating accurate comparisons. When emphasizing this point, we do not, however, forget that hand in hand with this quantitative work the qualitative tests have been marvelously refined, and that these necessarily form the foundation for quantitative work, since all such work must deal with the elements or groups of elements which can be sharply defined, and the basis for their definition is given through qualitative studies. As progress is made along these lines, we appreciate more and more that it is of importance for us to know not only how much brain and how much spinal cord by weight normally belong to a given species of animal, but also the *quantitative relations* of the different groups and classes of elements which compose these parts. We are continually asking ourselves how far the range in gross weight of the central nervous system may be dependent on changes in the number of elements in the different divisions or localities, and how far dependent on the mere increase in the bulk of the individual units without any change either in their absolute number or relative size. Work along this line rests as we know on the neurone theory, that epoch-making generalization concerning the structure of the nervous system which was put forward by our honored colleague Professor Waldeyer.[1] Most of us are aware that, at the moment

[1] Waldeyer, *Deutsche medicinische Wochenschrift*, 1891.

this theory is the subject of lively and voluminous discussion, and that Nissl,[1] for example, urges the inadequacy of the conception on the ground that it does not account for the gray substance in the strict sense.

No one can fail to appreciate the very great importance of the satisfactory conclusion of the present dispute, and earnestly desire that we may obtain conclusive evidence on points involved; but how ever the question of the gray matter may be settled, the enormous importance of the neurone conception, and the value of it for the purposes of the microscopic analysis of the nervous system, will remain untouched, while our quantitative determinations, applied to the neurone as we now understand it, will still have a permanent value.

Returning to the questions which are raised by the previously mentioned investigations of Dubois, we require in the first instance to determine the number of neurones connecting the skin with the central nervous system, and to see how this number varies in the different species of mammals similar in form but unlike in size. There is only one animal, the white rat, on which as yet such studies have been made, so that the whole field lies practically open. Should we be able to get good numerical evidence in favor of the view that under the conditions named above the afferent system could be taken as an index of the size of the brain, it would show us at once that in the laying-down of the nervous system certain proportions were rather rigidly observed, and bring us to the next step, namely, the determination of the influences which control those proportions and the possibility of effecting an alteration in them. In the mean time, there is every reason to prepare for the application of these results to man, and although the programme here is simple enough to state, it will involve great labor to carry it through.

So far as the numerical relations in man are concerned, we have, through the work of Dr. Helen Thompson [2] an excellent estimate of the number of nerve-cell bodies in the human cortex, and through that of Dr. Ingbert,[3] a reliable count of the number of medullated nerve-fibres in the dorsal and ventral roots of the thirty-one pairs of spinal nerves of a man at maturity. It is easy to see, however, that we must get some notion of the amount of individual variation to which these relations are subject within the limits of one race and one sex before it is desirable to attempt to learn whether the difference in race or sex here plays an important rôle. It is to be anticipated, however, that the differences dependent upon race and sex will be comparatively slight, and especially so when contrasted

[1] Nissl, *Die Neuronenlehre und ihre Anhänger*, 1903.
[2] Thompson, *Journal of Comparative Neurology*, 1899.
[3] Ingbert, *Journal of Comparative Neurology*, 1903 and 1904.

with the differences which we may anticipate as existing between the adult and the child at birth. This aspect of the problem illustrates, in a concrete form, the sort of question which is raised by the anatomical study of the body during the period of growth. The embryologists have worked out the formation and early developmental history of the various organs and parts of the human body, but the study of the later fetal stages have been blocked by the scarcity of material, and the inconvenience of dealing with it. On the individual at birth, we have again more extensive observations, but for the period comprised between the first two years of life and the age of twenty our information is again scanty. The lower death-rate during this part of the life-cycle, as well as social influences, combine to keep material between these ages out of the dissecting-room. Here is an important part in the life-history of man which needs to be investigated along many lines, and during which it is most desirable to have a record of the changes in the nervous system expressed in quantitative terms. In the general problem which is here under discussion, our next step would be to enumerate in man at birth the medullated nerve-fibres in the roots of the spinal nerves. Such an enumeration will probably show us between birth and maturity a very large addition to the number of these fibres, but we still have to determine at what portion of the period, and according to what laws this addition takes place. At this point our observations on animals will assist us, and we should certainly look for the occurrence of greatest addition during the earlier part of the growing period.

Let us assume, then, that we have obtained results which show us the normal development of this portion of the nervous system between birth and maturity. These observations could be used as a standard. Once possessed of such a standard, we are prepared to determine variations in the nature of excesses or deficiencies, and in this instance the question of deficiencies is the one most easy to handle.

The studies of Dr. Hatai [1] on the partial starvation of white rats during the growing period show that very definite changes can be brought about in the nervous system when these animals are deprived of proteid food for several weeks. As a result of such treatment, the total weight of the nervous system is reduced much below that of the normal rat. Such a result, however, leaves two points still undetermined: (1) the general nature of the changes bringing about a diminution in weight, and (2) the parts of the system in which changes occur. In testing our animal material by quantitative methods, we should in the first instance direct attention to a possible decrease or arrest of growth in the afferent system of

[1] Hatai, *American Journal of Physiology*, 1904.

sensory nerves, and seek to determine whether the unfavorable conditions have not retarded the growth-process in this division of the nervous system. If the results of such observations are positive, we may expect to find a corresponding modification in man, when the human body during the period of growth is subjected to unfavorable conditions of a similar nature. As a matter of fact, such unfavorable conditions do exist in the crowded quarters of our larger cities, and it seems highly probable that we have there in progress examples of partial starvation quite comparable with the experiments conducted in the laboratory. Under these circumstances, it is important to discover in the case of our animals how far a subsequent return to normal food conditions will modify the anatomy of a nervous system which has been subjected to proteid starvation for some weeks. At present there are no observations which indicate whether or no recovery in the nervous system will take place, and it will probably require some time to reach a definite conclusion. The work necessary for a determination of the anatomical changes exhibited by the animals alone constitutes by no means a light task, since in order to obtain reliable results and to eliminate the factor of individual variation a series of individuals must be examined, and it requires a very definitely sustained interest to carry through the long line of enumerations necessary for such an investigation. The examination of the growth of the nervous system in animals subjected to definitely unfavorable conditions is, however, only one part of the work.

It will be necessary to contrast the changes there found with the effects of special feeding, care, and exercise in other groups, in order to see how far above the ordinary form the nervous system can be anatomically improved by any such treatment; and experiments in this direction are already being conducted by Dr. Slonaker. Of course, the results which have been obtained and may be obtained on the animals studied in this way should not be directly applied to the case of man, because it seems quite evident that the higher organization of man is responsible for his ability to resist to a remarkable degree the disturbing effects of an unfavorable environment. The impression is abroad that the reverse is the case, and that it is man who is more responsive to unfavorable surroundings. I believe, however, that this current view will prove to be incorrect, for the lower mammals at least, and that when we place such animals where the conditions for them are abnormal, their limited powers of adaptability lead them to be more seriously affected than are animals which are more complexly organized. If such is the case, variations of the same amount should not be expected to appear in man, but there is every reason to assume that the variations which do appear will be of the same general character, and that we might look for them in the human nervous system where we find them in that of the rat. When it is possible to see how the anatomy of the nervous system may be altered during the post-natal growth-period, we shall be prepared to take up the problem of how it may be improved during embryonic and fetal life, and how the actual number of potential neurones is determined and their relative distribution controlled, and this should lead ultimately to the attempt to breed animals with improved nervous systems in which we shall know the nature of the improvement in considerable detail.

It may be urged that putting the problems in this way indicates a greater interest in the application to physiology of the anatomical results than in the results themselves. But I take it that the interest of a machinist in building a machine is to make the parts for one that will go, and that no less honor is due him for his painstaking care in determining the construction of the different parts and their right relations, because at the end of the operation he has devised something capable of doing work. Similarly it is possible that a man's interest from day to day shall be absorbed in the technique of anatomical science, and yet, it is nevertheless distinctly advantageous, if his anatomical observations bear on the performances of the living animal, and a final result is obtained which is the synthesis of research in two associated fields.

In drawing up the preceding outline, no one is more aware than the writer of the fact that problems connected with the nervous system have alone been considered. Without doubt those more interested in the other systems of the human body could duplicate for these the problems which have been suggested in connection with the nervous system, so that the account given above may be taken simply as an illustration of the sort of thing that seems worth doing. In presenting these illustrations it has been my purpose to indicate a standpoint from which the anatomical problems can be profitably regarded, and to draw attention to the use of quantitative methods in the study of anatomy, and especially as applied to the body during the period of active growth.

Yet perhaps the largest of our problems, and certainly one which appeals to all of us, is the ways and means for the solid advancement of our science. Alongside of the question of how we shall hand down to successive generations of students the facts already established, lies the still more fundamental problem of the best method of building-up the body of anatomical knowledge.

It is not my purpose to advocate as a means to this end the sharp separation of teaching from investigation. It is a rare man who can stand the strain of such a division, whether he chooses one or the other, and there is, moreover, much to be said for such an arrangement as will bring the average student into a laboratory where he can himself see how research work is conducted. Yet it would be possible to name institutions in which the relative amount of time required for teaching as compared with that left free for investigation might with advantage be readjusted, and almost all of our educational institutions at the same time admittedly lack the funds and often the educational purpose, which would justify them in attempting to meet the various difficulties connected with anatomical investigations on a large scale. Yet no one questions the importance of striving for a more rapid advance. A response to this feeling finds its expression in the several research funds which are now available in this country and abroad for the endowment of investigation, and in the plan presented to the International Association of Academies, and, it should be added, largely due to the initiative of Professor Waldeyer, for the establishment in various countries of special institutes for the furtherance of research in embryology and neurology.

These two subjects were first selected owing to the peculiar difficulties of obtaining the needed material, and the great labor necessary to prepare the complete series of sections which are required in many cases. These conditions make it imperative that, if we would avoid large loss of labor and much vexation of spirit, the work in these lines should be coördinated, standards adopted, and the material of the laboratory, like the books of a library or the specimens in a museum, be available for the use of other investigators. Nothing, I believe, is further from the minds of those engaged in this plan than an attempt to produce anatomical results on a manufacturing scale. But the questions calling for solution in the fields here designated are so numerous that such an arrangement will merely mean a subdivision of labor in which each institute will take one of the larger problems and direct its main energies to the study of this, so conducting the work that it shall be correlated with that in progress elsewhere. The director of such an institute will be justified in extending his work through assistants just as far as he can carry the details of the different researches in progress, and thus knit them into one piece for the education of himself and his colleagues. When we pass beyond this limit, admittedly subject to wide individual variation, there is little to be gained, but the evils of excessive production, should they arise, carry within themselves the means of their own correction.

This step, which is assuredly about to be taken, should enable us in the future to do things in anatomy not heretofore possible, and when, some years hence, there is another gathering of scientific men, with an aim and purpose similar to that of the present one, it is easy to predict that we shall be able to listen to a report on the important advances in anatomy arising from coördinated and coöperative work.

SECTION K — PHYSIOLOGY

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(*Hall* 4, *September* 23, 10 *a. m.*)

CHAIRMAN: DR. S. J. METZER, New York.
SPEAKERS: PROFESSOR MAX VERWORN, University of Göttingen.
PROFESSOR WILLIAM H. HOWELL, Johns Hopkins University.
SECRETARY: DR. REID HUNT, Washington.

THE Chairman of the Section of Physiology was Dr. S. J. Metzer, of the Rockefeller Institute, New York City, who took for his introductory topic :

THE DOMAIN OF PHYSIOLOGY AND ITS RELATION TO MEDICINE

PHYSIOLOGY is of medical parentage, was reared by medical men, and is still housed and fed by medical faculties. Yet it is medicine against which its frequent declaration of independence is directed. Medicine is a practical science, and is too inexact, and physiology wishes to be a pure, exact science. It, therefore, tries to keep aloof from medicine, and manifests a longing for association with, or, still better, for a reduction to, physics and chemistry. It urges, furthermore, that the affiliation with medicine binds physiology down to only one species of animal with intricate, complicated conditions, while it would be more beneficial to physiology if it would direct its energies toward a study of monocellular organisms where the conditions are so simple.

Permit me to discuss briefly the domain of physiology and the importance of its relations to medicine as they present themselves to my mind. There can be no doubt whatsoever that physiology has a perfectly legitimate object entirely of its own. Perhaps I may elucidate this statement in the following crude way. All natural phenomena impress us in two ways, — as matter and as force. The phenomena are either inanimate or animate. The studies of inanimate matter are to be found in mineralogy, crystallography in a part of chemistry, etc. The studies of the forces or energies of inanimate phenomena are carried on by physics and physical chemistry. In the fields of living phenomena, matter is studied by gross and minute anatomy and by descriptive zoölogy and botany, or, in short, by morphologyy. The studies of the forces, the energies, or the functions of living matter are the proper domain of physiology. Now this definition permits a few deductions. All these four divisions are bound, as sciences, to have something in common in their methods of investigation; they must employ the inductive method, and must strive to reach in their results that degree of certainty which the nature of each individual science permits it to attain. But the four divisions differ greatly from one another; each one has its own subjects and laws and its own problems, which have to be solved by methods peculiarly adapted for each division. It is certainly clear to every one that it cannot be the essential task of animal morphology to reduce itself to mineralogy because it can be demonstrated that some anatomical objects contain lime and other mineral substances. It seems to me it ought to be also clear to every one that it cannot be the sole task, and not even the essential task, of physiology to reduce itself to physics and chemistry because some or many of the living phenomena are governed to some extent by known laws of physics and chemistry. Physiology has to study the functional side of life, and in the attempts to elucidate its complex phenomena it certainly has to employ also the known facts of physics and chemistry. But if we would confine the domain of physiology to such parts only which can be interpreted by the laws of physics and chemistry of to-day, we should have to give up nine hundred and ninety-nine out of a thousand of the phenomena of life as still inappropriate for physiological study. The four divisions of the natural sciences are closely interwoven, and each one can, of course, profit by the experience of the others. Boyle, Mayow, Priestley, Lavoisier, and others attempted to unravel the nature of oxygen, nitrogen, and carbon dioxide gas by the aid of experimental studies of the physiology of respiration. The physicist or the chemist employs any method which would help him to shed light upon his subject, but physics and chemistry have methods peculiar to themselves, and that is the secret of their great success. And so it should be with physiology. However, when physiology broke away from medicine, it ran into the arms of physics and chemistry, and is still largely there. The early successes which have attended the new venture, which, by the way, is the case with every new venture, led to the conception that this is the most desirable, the most natural union. An analysis, however, of the work in animal physiology in the last few decades will show the fact that the too great gravitation towards physics and chemistry prevented the development in many directions of a purely physiological character.

I contend that physiology is an independent science with a clear outline of its domain, but it ought to direct its declaration of independence not only towards medicine, but also towards such exact sciences as physics and chemistry.

As to the standard of precision and exactness to be required of physiology, let me say this. Certainly no physiological problem can be solved with that exactness, with that absolute reliability which is now the standard for a good many problems in physics and chemistry. Above all, in the studies of the energies of life we lack the controlling factor of synthesis. If we can produce synthetically urea or sugars or other dead constituents of a dead or living body, we cannot yet make synthetically the smallest living organ of the smallest homunculus. But what of it? Each science has its own degree of attainable exactness. Physics and chemistry have one standard, and paleontology or geology is bound to have another standard of exactness. There is no one standard of exactness for all sciences. The scientific demand upon work in any science is to strive for that degree of exactness which is attainable in each specific field of investigation.

I contend, further, that physiology ought not and cannot be properly developed upon the basis of a morphological unit. We might just as well attempt to put up the mineral crystals as a basis for the study of physics.

I may say, further, that in my opinion the knowledge of vital energies would progress more rapidly if we were guided in our investigations by the view that the actual processes in the phenomena of life are of a very complex nature. The desire to reduce the multiplicity of phenomena to a few simple principles is a philosophical importation of a psychological origin. Certainly premature attempts to offer simple interpretations for complex phenomena have often been an obstacle for a further development of our knowledge of the actual processes.

Physiology, however, may take some useful hints from the other sciences. It may learn from such exact sciences as physics and chemistry that the exactness and dignity of a science do not suffer by coming into intimate contact with the necessities of daily life. On the contrary, we find that those chapters of physics and chemistry whose results found practical application are best developed. The contact of a science with life and its actual necessities works, on the one hand, as a stimulus to investigation, and, on the other hand, as a corrective against an indulgence in mere hobbies. The experimental method as such is no talisman against such scholastic degeneration. A study of the literature of the last few decades will show that physiology, too, could well stand such a corrective.

Physiology could also learn from morphology that a special attention to the human being does not necessarily lead to a neglect of the uniform study of the entire animal kingdom. The marvelous complete studies of gross and minute human anatomy, which was of such immense service to pathology and surgery, was in no way an obstacle to the brilliant development of the broad science of zoölogy.

There is, however, one difference between the studies of the energies of inanimate phenomena and the studies of the vital energies, to which I would like to call special attention. For physics there is only one kind of energies; they are all normal. If the physicist meets with conditions which apparently do not agree with some established law, he does not transfer these conditions to a pathologist in physics for further investigation. On the contrary, he is only too glad to have such an opportunity; it usually leads to an elucidation of the old law, or, still better, an entirely new law might be discovered. When Kirchhoff was surprised by the apparently contradictory fact that by the addition of the yellow light of sodium to the sunlight the dark *D*-lines in the spectrum, instead of becoming lighter, became still darker, he did not turn away from the problem. On the contrary, he was glad of this opportunity; in fact, as he stated once, he was longing to meet such a complete contradiction. The result was the establishment of the law of the proportion between emission and absorption of light and the creation of the nearly new science of spectral analysis. Or, to quote a more recent instance, the exceptions to van 't Hoff's law of osmosis which were met with in salt solutions and which had been displayed by some as a proof against the validity of that law, served Arrhenius as a basis for the establishment of the far-reaching law of electrolytic dissociation. It is totally different, however, with physiology. Its domain is, as we saw above, the study of the functional side of living phenomena. Here, however, we find the artificial and unsound distinction between normal and abnormal functional phenomena. Physiology set up some laws; and if conditions appear which do not fit in with these laws, physiology declines to deal with them; it refers you to medicine. Are the laws governing the vital functions under pathological conditions actually different from those controlling the functions in health? Certainly not. The laws which physiology establishes must be capable of covering the functional phenomena in all conditions of life. The apparent exceptions in disease should serve in physiology, as in physics, to unravel the real nature of the laws governing the functions of living phenomena, whether they occur in health or in sickness. For instance, the processes occurring while the body is in a state of fever should give a clue to the understanding of the mechanism of the constancy of the elevated temperature of warm-blooded animals. Or the conditions prevailing when urine contains albumin should be seized as a means of studying the remarkable phenomenon in the normal urinary secretion, namely, that of all the endothelial cells of the body the kidney endothelia alone do not permit normally the passage of albumin. Or the conditions of the blood and the lung tissues in pneumonia could serve as an aid in studying the factors concerned in the formation of fibrin. And so on and so on in many thousand instances of daily occurrence. Some very important discoveries in physiology were thus recently brought to light through medical experience and by medical men, with hardly any aid from physiology. The anatomy of the cases of myxœdema and cretinism and the results of the complete removal of the thyroid gland for goitre revealed the physiological importance of that ductless gland for which physiologists, with one single exception, had no interest. This discovery helped at the same time to establish and to introduce into physiology the far-reaching conception of internal secretion. Furthermore, the observation of Bouchard, Lancereaux, and other medical men of the occurrence of a degeneration of the pancreas in cases of diabetes mellitus, led to the discovery, by two medical men, of the remarkable fact that the complete removal of the pancreas in dogs leads to diabetes. This discovery demonstrated at the same time the further principle that even glands with a distinct external secretion have besides a physiological importance for the body by virtue of their internal secretion. In the long list of workers on this subject we hardly find a single physiologist.

I could quote a good many more instances in which medical studies brought out important physiological facts and how physiology is slow to avail itself of such golden opportunities.

The physicists are only too glad to meet with exceptions; the physiologists run away from them. Is there any well-founded justification for such a course in physiology? I believe none. I believe it is simply an erroneous position. It would lead me too far to attempt here a discussion of the causes which led to this position in physiology. But I say without hesitation that this position is deplorable, is harmful to physiology as well as to medicine. Animal experimentation is the essential method of developing physiology. Now, then, nature makes daily thousands of experiments upon man and beast, and physiology refuses to utilize them for its own elucidation. I feel quite sure that a study of the functional processes in pathology, or at least the systematical taking up of physiological problems indicated by pathological processes, by minds naturally endowed and properly trained for physiological studies, would greatly elucidate the proper sphere of physiology itself, and would at the same time be of incalculable value to pathology and medicine.

And medicine is greatly in need of such a physiology. I am afraid that the actual situation in medicine is not fully grasped, even by a great many of its enlightened disciples. To state the critical point in a few words: The actual disturbance in most of the diseases is primarily of a functional nature, but the essential part of the present knowledge in medicine is morphological in its character! This discrepancy is due to the uneven development of the sciences of medicine. When the empirical art of medicine awoke to the necessity of acquiring a scientific basis, it found ready for its disposal an already well-defined, precise anatomy, but only a vague, incoherent physiology. It set out and continued to work in the precise lines of anatomy, in which it attained a marvelous completeness. By this step, however, morphology became the dominant factor in medicine, and the definition of a disease became inseparably coupled with that which was found in the body after it succumbed to the disease. When, at a later period, physiology also became a precise science, it broke away at the very onset of its regeneration from medicine; it wished to be exact, to be a pure science, and thus gained no influence upon pathology, which it refused to study. So it came about that medicine is made up of a complete knowledge of the anatomical conditions after death, of nearly a complete morphology of the symptoms of the disease during life, but of only a vague, makeshift mechanical interpretation of the functional disturbances during the actual course of the disease. The last decades have seen the birth and marvelous growth of the knowledge of the etiology of disease. Animal and vegetable invaders were recognized as the essential cause of many diseases. But the study of the functions of the body whose lot it is to grapple with the invaders received only a secondary attention, and that again essentially from morphological quarters. At the present time still more knowledge is being diligently added to the stores of medical wisdom. Chemistry has taken a powerful hand in the studies of physiology and pathology, and is attaining brilliant results. But we should not be misled. The studies are essentially morphological in their nature. It is physiological and pathological chemistry, and but very little chemical physiology and pathology. Even if the hopes of the new school of brilliant chemical investigators will, indeed, be realized, viz., that in a not far-off future they will know the structure of proteids and all their constituent bodies, it will be the knowledge of the proteids of the dead bodies, it will be a brilliant post-mortem chemistry. Living animal matter, however, is something else than dead proteids, as living plants are something else than carbohydrates, although the knowledge of the latter has already reached the ideal stage where some of them can be produced synthetically. No, a study of life, normal and abnormal, is essentially a study of energy, of function; of course, the knowledge of the underlying morphology, dead or living, is a prerequisite for such studies. And let me state right here that there seems to be a difference in the make-up of the human mind with regard to the different studies. Some are more apt and better endowed to grapple with the problems of energy, and others, again, have natural talents for the science of morphology. Only a few, however, have the good fortune of becoming educated in the lines of their natural endowments, and still fewer have the genius to work out their natural destinies against all odds, against all education and training. Now the men who did and who now do the original work in the medical sciences received their training in the studies of medicine, four fifths of which is profoundly developed, magnificent morphology. We cannot wonder, therefore, that most of the original contributions to the medical sciences are essentially of a morphological character. Even in the very recent brilliant additional departments of medicine, in bacteriology and chemistry, the research work is, as already stated above, for the most part of a morphological stamp. It is true that a few men of genius in medicine, Cohnheim, for instance, broke their acquired chains and made an attempt to study pathology from a functional point of view. Such attempts, however, were not many, and their permanent influence is not extensive. What is now termed general pathology or even pathological physiology consists, in the first place, of a collection of histological, bacteriological, and chemical facts of a general but essentially of a morphological nature, including at the same time the applications of a few well-established physiological facts to pathology and a few results from direct experimentation in pathology. That is not a study of physiology under pathological conditions, and certainly not a study of general physiological laws which can be stimulated by and derived from a study of pathological processes. And it is just this kind of study which is missing, and which could be developed only by a purposeful and concerted action of the men who have a training in the study of the functional side of life, among whom there are surely many who have a natural endowment for such studies.

The following review of the present situation in medicine will show us the place left vacant by physiology, and the disastrous consequences. The studies of pathological anatomy extend over all divisions of medicine, are lucid and nearly complete. Diseases which are exclusively due to palpable anatomical changes are quite well understood. Their harmful effects are, for the most part, of a mechanical nature. In proportion as they are understood, these forms of disease become amenable to an efficient treatment; it is mechanical, it is surgery.

The studies of the etiology of diseases revealed and continue to reveal many of the foreign originators of disease, the animal and vegetable invaders of the living organism. This new and lucid knowledge led again to some effective measures in the treatment of diseases, it led to clear plans in preventive medicine, it gave means to the surgeon to enter with impunity into the interior of living organisms, and in a few instances it discovered actual remedies for non-surgical diseases.

But most diseases are something more than mechanical disturbances, or exclusively anatomical changes. There is, in the first place, that large group of so-called functional diseases which has no pathological anatomy, and for which clinicians have very little interest. But even those numerous diseases in which the post-mortem examination revealed distinct anatomical changes were only results of the advanced stage of the disease. The disease during life consisted primarily surely in disturbances of a functional character, in reactions to foreign causes, reactions of living energies, the physiology of which we have possibly as yet not even an inkling of. The so-called organ physiology, which appears to the teachers of physiology to be so extensive that it can hardly be taught to students of medicine in one year's lectures, is of astonishingly modest assistance to the understanding of the actual processes of disease. For instance, in the present knowledge of the entire section of the diseases of the respiratory tract, physiology has hardly any share. The knowledge of the few physiological principles which are applied there can be acquired in one hour's instruction. The extensive knowledge in this chapter of pathology is essentially of a morphological nature. Do the functions of the involved organs take no part in these pathological processes? Most certainly they do; but we know too little of it, and the clinician passes over the gap with some makeshift mechanical explanations. The same is true in neurology; in fact, in nearly every chapter of internal medicine. It is impossible to dwell here on the particulars of our subject. What is the result? First-class clinicians employ their brilliant faculties in continually developing the morphology of diseases and their diagnosis. But treatment? There is either a nihilism pure and simple, or some sort of a symptomatic treatment is carried on with old or new drugs upon a purely empirical basis. Or there is a great deal of loose writing upon diet, air, water, psychotherapy, and the like, and a great deal of semi-popular discussion in international, national, and local meetings and popular prize essays on the best methods of treatment, — with a net result of only a very modest actual benefit for the poor patient, who, in addition to his affliction, has now to feel the tight grip of the modern health officer. There is no efficient treatment of internal diseases in any way comparable with the specific surgical treatment of mechanical diseases, no specific quelling, correcting, or curbing of primarily functional disorders. And there never will be such a specific functional therapy before there is a physiology which, like physics, will be only too glad to meet with many exceptions in order to understand properly all the rules by which the energies of all grades of living phenomena are guided.

THE RELATION OF PHYSIOLOGY TO OTHER SCIENCES

BY MAX VERWORN

(*Translated from the German by Dr. Thomas Stotesbury Githens, Philadelphia*)

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WHAT is physiology? Ask any educated person, who does not belong to the narrow circle of naturalists and physicians, concerning physics and chemistry, concerning botany and zoölogy, concerning anatomy and pathology, even concerning psychology, and you will receive an intelligent answer. Ask him, however, concerning physiology, and he is generally unable to give any information. It is the peculiar fate of physiology that it is the least known of all the great branches of natural science, even among the educated classes.

I have often asked myself why this should be. Why do the educated classes lack a clear conception of physiology? We may here think of several reasons. To me, however, it appears that one cause is of especial importance, that is, the one-sided limitation of physiology to its own special problems.

For a long time the great general questions have been neglected by physiology, the questions which interest the masses. Hardly another branch of biology requires specialism as much as physiology, which, in each of its different branches, requires such various and manifold preparatory education that the individual investigator must generally limit his work to a single branch in order to make any advance in the short span of his life. This is why the work of physiologists is not understood among the masses. Its connection with the great problems is generally not clear to them.

This one-sided immersion in special problems has even led to an isolation of physiology among those sciences which originally stood nearest to it. Physiology was, at one time, closely amalgamated with anatomy and pathology, with zoölogy and botany, with physics and philosophy. Even since the scientific renaissance of the sixteenth century, physiology stood in the closest connection with all these branches until far into the nineteenth. For a century, however, this connection has become looser and looser, and toward the end of the preceding century physiology was already almost entirely isolated. Indeed the isolating differentiation began its destructive work, even in its own special realm. This was the time when, in Germany, Hoppe-Seyler's efforts were directed toward the separation of physiologic chemistry as a separate science. If he had succeeded, the individual branches of physiology itself would have lost sympathy with one another. This danger now appears to be past, although now and then a voice is still heard in favor of the separation of physiologic chemistry. But even without this, the whole development of physiology is a classic example of the constantly increasing tendency of the present day toward differentiation of special branches.

At a time when the expansion of separate branches has reached as extreme a degree as at present, at a time when the immersion in certain special questions threatens to result in a complete loss of relationship, and, in fact, has already partly succeeded, at such a time the need of compilation makes itself more and more felt. This has already been recognized in this country, in which the restricting fetters of tradition and historic development do not weigh so heavily as in the Old World. Compilation was, therefore, the word which has brought us together to-day. As concerns my own branch, I must greet this tendency with especial joy. Perhaps the spirit of union, which is felt here to-day, will succeed in reviving the natural relations which unite physiology with so many other sciences, to the mutual advantage of all branches and to the furthering of human knowledge.

If I attempt in the following to sketch briefly the manifold relations of physiology, I will turn my attention above all to those relationships from which we may expect in the future especial advantages for the further development of our knowledge.

The natural relationships between physiology and other sciences follow of necessity from the aim which the former follows. Physiology is the science of life. In this conception there is universal agreement. We may clothe this naked definition in different garments, but its germ remains always the same. The general aim of all physiologic investigation is the analysis of the phenomena of life. We may ask, however, what principle should physiologic investigation follow in this analysis; but in regard to this there has not always been universal agreement. Different periods and different investigators have given different opinions. We have varied often between purely mechanical and more mystical principles. First one, then the other, has ruled alone. At times the adherents of the first, at times those of the second have increased. After a long period, full of valuable results, in which the purely mechanic consideration of life-phenomena ruled, the pendulum has swung again, in the last decennium of the past century, toward the side of mysticism. Certain investigators have felt that it was necessary to consider in scientific questions the tendency of the times, which in art and literature was toward mysticism. An attempt has even been made to revive the old doctrine of "life-power." This movement has ended in speculation and fantasy in the problem of development, which is not yet ready for experimental investigation. Among physiologists, whose daily experience brings immediately before their eyes the truthfulness of the mechanical conception, the mystical views have found no adherents. But especially in semi-scientific circles such words as "Vitalism" and "Neovitalism" have been considered the most modern in science and spread abroad with more energy than understanding. In opposition, the standpoint of scientific physiology is, to-day, completely clear.

In reality the matter is quite simple. The subject of investigation of physiologic experiment is the living organism. As naturalists, physiologists can only have the task of analyzing scientifically the phenomena of the living body. Only that which is perceptible is, however, accessible to scientific analysis, and nothing but perceptible objects can ever be the subject of scientific investigations. The general principles and laws of phenomena in the perceptible world are studied by physics and chemistry, and both have carried their knowledge to a high degree. The organism, as a perceptible object, must be subject to the general laws which rule the perceptible world, and, therefore, we cannot analyze the life-phenomena of organisms otherwise than according to the principles of physics and chemistry. Physiology is, in other words, the special physics and chemistry of organisms. As organisms are composed of the same elements which are found in the inorganic world, no other factors can apply than those which are seen in the inorganic world, and the special peculiarities of the organism can only be based upon the specific combination of physical and chemical phenomena, for physiologic analysis must finally go back to general principles, as only then is its task fulfilled. For mystic factors, not of a physical or chemical nature, there is no place in physiology; as they would not be comprehensible by human knowledge if they were not perceptible or with perceptible effects, and therefore would always remain hypothetical.

This standpoint has always given practical results. Everything which has ever been fixed by physiologic investigation has arisen from the practical application of this conception of physiology, as the physics and chemistry of the organism. "Life-power" has not made the slightest addition to the explanation of life-phenomena, in the entire development of physiology.

From the conception of physiology as the special physics and chemistry of the organism, arises of itself the extremely close connection with these two general natural sciences. Physics and chemistry ascertain the general laws which rule the perceptible world, and physiology analyzes the action of these laws in the special system of the organism, as geology studies the activity and force of general physical and chemical principles in the special system of the planets, or mineralogy in the special system of crystals and minerals.

The organism is, therefore, for the physiologist, only a special case of a system, which he must analyze according to the general principles of physics and chemistry. Physiology, therefore, receives from physics and chemistry its general conception of the laws of phenomena in the physical world. The more deeply physics and chemistry penetrate into the knowledge of general laws, so much more deeply can the investigation of the phenomena of life proceed. Physiology is, in this relation, entirely dependent upon the development of physics and chemistry, and must follow their progress attentively. To-day this is especially important. The rapid development of the great mass of facts and theories, which have recently been united under the name of "physical chemistry," appears to be destined to unite these previously independent sciences to a uniform scientific branch. A number of theories of a general nature have already been proposed which must have a marked influence on the investigation of the phenomena of life. The effect of this great progress in the realm of physical chemistry is already beginning to be felt in physiology. The recent conceptions regarding the nature of solutions, the theory of ions, the conception of osmosis and diffusion and of electrochemical processes, the knowledge of the laws of chemical equalization and the effect of mass, and many other new ideas, are already beginning to have as fruitful an influence upon the investigation of the phenomena of life as a half-century ago the discovery of the laws of energy exercised.

But the conception and symbols of physics and chemistry will be still further developed, and will be materially changed, in the course of time. We live to-day in a period in which the well-proved symbols of physics and chemistry, hoary with age, such as the conception of matter, of atoms, and of force, begin to waver. New symbols, new allegories, new conceptions will come in their place. It would, therefore, be illogical to expect that physiology could solve all the phenomena of life without fail, by the present knowledge of physics and chemistry. It is still far away from this goal. Physics and chemistry cannot explain quite all of the simpler phenomena of the lifeless natural world, with their present symbols. But however the conceptions of physics and chemistry may change in the course of time, one fact remains: no other principles can come into play in the world of organisms than enter into that of lifeless nature. Physiology can never be anything else than physics and chemistry, that is, the mechanics, of living beings.

It does not appear to be superfluous to warn here against one of the consequences which may occur from a short-sighted exaggeration of this conception of physiology. The aim of all the so-called exact sciences is, admittedly, the demonstration of laws in mathematical form. We occasionally meet with the view that, in the exact natural sciences, nothing shall be the object of investigation which cannot be measured according to mass and number. This conception is destined to hinder the development of scientific knowledge, as the first step toward the explanation of many phenomena can, in most cases, only be made by qualitative and not quantitative investigations. A weighing and measuring, a numerical demonstration, is often only possible after a certain number of qualitative communications have been made, and physics and chemistry have seldom arrived at great and accurate results without this pioneer work. In physiology the relationships are still more complex, as here we have to do with the most intricate system of processes which we know of in nature, and in large part the first work has yet to be done. Here, there is still less often the possibility of a determination according to mass and number, and, therefore, if we throw aside in hasty blindness the study of qualitative relationships, we cast away, ourselves, the place on which we must set our feet firmly before we can climb higher. Physiology must still leave a large place for qualitative investigation, although the ideal goal is mathematical demonstration of the processes in the living organism, from which we are still far removed. It would be extremely ridiculous to attempt to determine a definite method for physiologic investigation. All schemes will do harm. Every means, every method, must be welcomed, if we wish to make even a small step forward. Therefore, physiology is not merely limited to the methods of physics and chemistry, but will always seek after the peculiar methods which are required by its special problems, although the problem of physiological investigation is only the mechanical analysis of life.

Man is for man the most interesting object of study. No wonder that the analysis of life was begun directly upon man, without considering that he is the most complicated and most difficult of all objects. The beginnings of sciences are never systematic, as their methods, problems, and aims are only seen in the course of their development. Thus it was seen later that mechanical analysis of the phenomena of human life could only be reached by investigating and analyzing analogous phenomena in other living objects, in the simplest forms. Geniuses did this earlier, of course. Harvey, Leeuwenhoek, Swammerdam, Malpighi, Redi, and others, are among the first of the comparative physiologists, although Johannes Müller and his contemporaries were the first to emphasize the necessity of comparative anatomy and of comparative methods in physiology. Physiology of man requires a physiology of animals.

Plant physiology developed itself independently as a necessity of botany, and this independence has remained almost complete, until very recent times. Each has made its way without much consideration of the other, but to-day they have many points of contact. Immersion in special problems, especially on the side of animal physiology, has, however, hindered general interest in its development. Only in recent times has the need of general physiological points of view succeeded in bringing the two branches closer to one another. The late but strong development of a general physiology, which, in contrast to special physiology of man, of animals, or of plants, sees its task in the analysis of the phenomena of life common to all organisms, is here the uniting band which previously was completely lacking.

The comparative method in physiology, as it flourished at the time of Johannes Müller, should have led sooner to the development of a general physiology, for it certainly pointed out the way toward it. But the great discoveries in the special branch of human physiology, which the second half of the preceding century brought forth, delivered the comparative method completely into oblivion, and the efforts in this direction were thus abruptly interrupted. At the same time were lost the relations of physiology to zoölogy, which before had been most intimate. Every one-sided development, however, experiences a modification, when it has reached a certain point, by a process which is to some extent automatic. The defect increases more and more, until finally, of itself, it impels this corrective process. This is what we see to-day. General physiology has suddenly begun to develop itself rapidly.

A renewed study of morphology supplied the impulse. The great discoveries of Schleiden and Schwann gave morphology a different appearance and could not remain without influence upon physiology. The construction of organisms from structural elements similar throughout, forced the conclusion that the processes which occur in the individual structural elements are merely the external life-phenomena of the organism. Thus, every physiologic problem must finally end in a study of the cell, and the cells, as the general structural element of living substance, attain an especial interest for physiology. The cell is the seat of the actual life-processes, which shows us life in its simplest form and includes in itself all the secrets of living substance. We must know what occurs in the cell, and study its general physiology.

But the life-phenomena of the different forms of cell show themselves not less manifold than those of the great, many-celled organisms. The general physiologic properties of cells must be recognized and be distinguished from the specific life-phenomena of separate cell-forms, and this is only possible by use of the comparative method. The different sorts of free living and tissue-building cell-forms, from the animal and plant kingdoms, became the objects of physiologic study, and a mass of general physiologic facts resulted from these investigations. The general physics and chemistry of the cell led us deeply into the knowledge of the general phenomena of life.

But we are only at the beginning. The new discoveries of physical chemistry give, for the analysis of cellular life, new points of view and new methods. The phenomena of assimilation and dissimilation, the facts of chemical balance, the disturbances of this balance by external factors, the inner automatic renewing of assimilation, the general effects of irritants, and many other phenomena of general physiology, begin more and more to lift their veils. New experiences stream toward general physiology, from the most various sources, which must crystallize themselves around the different parts of the system, after a firm nucleus of phenomena and facts has been determined to connect them. Thus the realm of general physiology grows larger and larger, and begins to break down the isolation of physiology among the biologic sciences. Let us guard the new branch of general physiology from being overtaken by the old fate of physiology, one-sided development. This is only to be avoided if we constantly keep before our eyes its great aim, the mechanical analysis of the general phenomena of life.

Before all, it is to be desired that general physiology may develop its own special problems as freely as possible, unhindered by attention to special problems and methods. The analysis of the general phenomena of life can easily lead to one-sided methods and one-sided points of view. Even the cellular investigations of general physiologic problems can degenerate selfishly. Here we must be sure to take into consideration the most varying cell-forms, and we must not merely consider individual cells, isolated as such, but also the general relationships and connections which arise from the communistic life of cells and the mutual influence of life-processes in the cell community. The investigation of the dependence of cell-life upon the surrounding life-conditions and the effect of every change of life-condition upon the life of the cell itself is of the greatest importance for the explanation of the immoderately complicated processes in the complex organism.

Also, in regard to methods, there must be no one-sidedness in general physiology. The great results of physical chemistry threaten general physiology with the danger of only working by that method.

That would be a mistake. We must not cast aside the old methods of chemical analysis and physical investigation. A science must not base its existence upon only one method, as a science only lives as a problem, and the problem of physiology requires the most manifold methods, according to the position of the question at the time. General physiology will only flourish as long as it retains the many-sidedness of its methods and its objects; but as long as it flourishes, so long will physiology retain its connection with the other biologic sciences, and at the same time form the connecting link between biology and mechanics.

In another direction, also, general physiology seems to be destined to act effectively in reviving old natural relationships, namely, in the realm of medicine. Physiology is one of the daughters of medicine. At first its existence depended on the needs of practical medicine, until Galen, whom we may call the father of scientific physiology, recognized clearly that the complete development of medicine is not possible, if it is not based on the phenomena of normal life. Physiology since his time has always retained more or less close relations to medicine, but has gradually developed itself to an independent science with its own aims. To-day we see the plainest expression of this historic relationship between physiology and medicine, in the fact that in most countries physiology in the universities belongs to the medical faculties.

The relationship between physiology and medicine has become now closer, now looser. In the last decennium of the past century it has become somewhat looser, but physiology has always retained its place in medical instruction. We find, even in old tradition, the view generally expressed that physiology is one of the bases of medical learning, but a view is now found among many that physiology is to a certain degree a luxury, a decorative element of medical science. If we examine the average well-educated practicing physician to determine what in reality is of use to him in his knowledge of physiologic phenomena, we find very little. A few indistinct impressions concerning the principal functions of the organs, and a few superficial chemical data which he has himself adapted "so as to make them of use in practice." That is all. Of the actual processes in the organs, tissues, and cells of the body, of the extremely close and important correlations of different parts which lie at the basis of the preservation of the entire mechanism, he has no idea. In order to reach this result a two or three semesters' study of physiology is not required. Actually physiology, apart perhaps from the branch of metabolism, has been overtaken by a certain isolation among the branches of medicine. Why is this?

Again we see the same cause. For a long time special subjects have stood in the foreground of physiologic interest, which have little or nothing to do with practical medicine. What an immense extent the investigation of the production of electricity in muscles and nerves has reached, in the physiological laboratories and lectures, and what could and can practical medicine do with these things? What an exaggeration Ludwig's discovery of the graphic method for the representation of motions has called forth in the physiologic instruction of the physician? We have even heard the opinion expressed that only that which could be demonstrated graphically should be taught in physiology. Yes, many physicians believe that they must go to practice with a Marey's sphygmograph in their pocket. And of what use have all these sphygmograms and respiration curves been in modern practice? They have disappeared. The graphic pocket apparatus lies among the old rubbish. Practical medicine has cast aside the false exactness which was imposed upon it. Instead of these, it has itself created general physiologic conceptions. Our entire knowledge of the physiologic protection of the normal body against infection, our whole experience with regard to artificial and natural immunity, which plays so dominant a rôle in modern medicine, did not arise from physiologists. The enormous development of this whole branch of medicine shows plainly the need of medicine for physiology, and especially for basic and general physiologic conceptions.

It appears to me that general physiology may have a very stimulating effect upon the further development of our medical opinions. There is one branch of medicine with which physiology has the very closest relationship; that is, the teaching of stimuli and their effects.

It is really a very paradoxical phenomenon, that physiology has worked for centuries with various methods of stimulation in their largest as well as in their smallest relationships, without ever investigating systematically the general laws of the effects of stimuli, without even attempting a sharp and general definition of the meaning of stimulus. Only the more recent development of physiology has brought about a closer approach to this question, and has already extended the truth to a certain degree, although many important points still wait explanation. The study of the effects of stimuli, in a large number of the most different independent and tissue-forming cells, has here permitted a fairly definite determination of laws, and, above all, has permitted the sharp fixation of the general conception of stimulus. To-day we can define this, in its most general sense, as a change in the external influences which affect the existing condition of a living system. Thus, the effects of stimuli find their expression in a quantitative or qualitative change of the existing processes of life. The latter group of effects is less extended in the normal life of the adult organism, and until now has been least studied. It appears, however, as far as we can determine from an extensive analysis, only as a secondary result of primary stimulation of the first group. The great mass of stimuli in the course of the life of the normal organism only cause quantitative changes of phenomena already existing in the living system, *i. e.*, either an increase of the same (excitement), or a decrease (paralysis).

The analysis of the effects of stimulation has now gone much further. I must, however, limit myself to-day to the most general indications. I will only be able to show how extraordinarily important this analysis is for the basic question of medicine, — what is disease? Disease is nothing else than life under changed external relationships, *i. e.*, life under the influence of stimuli. Thus, pathology comes finally to be a study of the effect of stimuli, and it needs no argument to show that the physician cannot penetrate too deeply into the knowledge of the effects of stimulation and the laws governing them. Above all, medical diagnosis, which by many physicians is considered the most important part of medicine, requires a comprehensive knowledge of the laws of stimuli. The physician must ask himself at the sick bed, what part of the organism is primarily affected by a stimulus? Does the effect consist in a quantitative change, an excitement or paralysis, or in a qualitative change of the normal life-processes? How may this change of the affected part act upon neighboring or distant parts of the body, as a result of the correlation of all the elements in the body, and how will the entire vital mechanism of the organism be disturbed? Those are the fundamental questions which every physician must lay before himself in a given case, if he wishes to have a fitting conception of the disease. Only then can he use his therapeutic means effectually. But it is not necessary for me to emphasize that this analysis must proceed as far as the cells themselves. A greater than I, almost a century ago, demonstrated so convincingly this requirement of pathology, that our entire present-day medicine rests upon the basis of cellular pathology. Since the epoch-making work of Rudolph Virchow, cellular pathologic investigation has developed almost exclusively toward the side of morphology, not toward that of physiology. A picture of a microscopic preparation of the diseased part, beautifully colored, with red or blue nuclei, etc., floats before the eyes of the well-educated physician, at the sick-bed. It does not occur to him, however, that the cells which he sees in imagination are alive, and he overlooks completely the chemistry of healthy and diseased cells. This is the place where general cellular physiology must come in, and here general physiology must come into the closest relation with medical diagnosis, if further progress and deeper knowledge are desired.

But therapeutics can, as little, do without an accurate knowledge of the effects of stimuli. The fundamental peculiarity of living substance, automatic regulation, is of the first importance for therapy, as Ewald Hering first showed clearly. If any stimulus has disturbed the balance of normal metabolism or kinetics, it restores itself immediately after the cessation of the stimulus, unless the latter has exceeded certain limits, in which case death results. The therapeutic test of the physician consists to a great degree in preventing the harmful effects of stimuli, for the organism cures itself. "Medicus curat, natura sanat." Naturally the use of any therapeutic measure requires the same profound knowledge of the phenomena of stimulation, for every therapeutic influence upon the organism is, essentially, a stimulus. And it is evident that the physician should only use stimuli whose effects he knows accurately, if he will effect a definite result of stimulation, for therapeutic purposes. For this reason pharmacology and toxicology, as well as therapy, base a large part of their usefulness on the phenomena and experiences of the physiology of stimulation. If they will proceed in a truly scientific manner, they must answer the same questions, and proceed in the same way, in the demonstration of the effects of medicaments and poisons, as that which was described in connection with diagnosis. Thus, in the whole realm of medicine, we are more and more forced to the necessity of the closest union with general physiology.

I might conclude here, but I feel that I should touch at least superficially a question which is much discussed to-day, that of the relation between physiology and psychology.

You will say, if physiology is the study of the phenomena of life, it must include psychic as well as physical phenomena, and psychology is thus nothing more than a branch of physiology. But the question is really not so simple; the psychic phenomena of any other organism are, of course, accessible to our mechanical analysis, but in the analysis of our own psychic phenomena we must put aside the principles and methods of physics and chemistry. Also, it has been shown that the chain of physical occurrences in the organism cannot undergo an interruption of continuity anywhere, not even in the brain. A physical process is always, and only, the result of another physical process, and the starting-point of a third. Thus there remains in the series of physical processes no place for any psychic link. We have, however, demonstrated that psychic processes only occur when definite physical conditions are fulfilled, so that the question concerning the relation of physiology to psychology is in reality nothing more than the ancient problem of the relation between body and soul.

Since the beginning of human thought, man has striven to solve this problem, but one attempt after another has been shattered. At times it was thought that the solution had really been found, but the old problem was always found smiling scornfully from the other side. The alchemy of the Middle Ages busied itself with this question, as it attempted to prepare gold from baser metals. Time and again the yellow metal shone forth from the crucible, but finally it was always found to be nothing but golden pigment. Perhaps our efforts are like those of the alchemists, and all our straining is useless, because the problem cannot be solved; perhaps the problem is like those of ancient times, such as the squaring of the circle, or the discovery of perpetual motion, which are in reality not true problems. Perhaps what Mephistopheles says is true,

> "O glaube mir, der manche tausend Jahre
> An dieser harten Speise kaut,
> Dass von der Wiege bis zur Bahre,
> Kein Mensch den alten Sauerteig verdaut."

Whence arises this conception of a dualistic relation of soul and body? We are accustomed to hearing Descartes mentioned as its source. I believe this is wrong. It is true that Descartes has most sharply defined dualism when he contrasted the body, as that which has dimensions, with the soul, as that which has not dimensions. But the concept is much older. We find it already in the philosophy of the ancients. It is not true that the dualism of body and soul is foreign to the thought of primitive man. On the contrary, the thought of a contrast between body and soul is very generally distributed among the primitive peoples of the earth, from Greenland to Tierra del Fuego; from the negroes of the tropics to the inhabitants of the South Sea. This shows that we have here to do with one of the most ancient thoughts of mankind.

The imaginative life of primitive peoples shows us plainly the origin of this dualistic conception. It is the sharp contrast between life and death, between waking and sleep, which led to the thought of a soul present in the body, a soul which may leave the body and again return to it, a soul which after death leads a shadowy existence as a spirit. This group of ideas, around which the entire spiritual life of primitive peoples revolves, has even developed into the conception of two distinct souls, in many of the Indian and Eskimo races. One of these, the perceptive spirit, which may occasionally during lifetime leave the body and enter other bodies, for instance in sleep and in dreams; the other spirit, which retains life, which passes away with the last breath, and, floating in the atmosphere, influences the fortunes of mankind, as a spirit.

"Zwei Seelen wohnen, ach, in meiner Brust;
Die eine will sich von der andern trennen."

But are these reasons, which gave origin to the twofold, or even threefold division of human nature, still binding for us? I answer no. The contrast of body and soul exists not at all. It is a deception. If we prove anything that we know in the entire physical world, if we analyze any existing substance, we find nothing but a sum of impressions. Impressions are, however, psychic elements. Hume actually believed that there was nothing to our bodies, except merely impressions, and Kant drew his "Ding an sich" from this conception. This was pure hypothesis, and Kant himself understood that the "the thing itself," must always be inaccessible to our knowledge, and that all knowledge must remain limited to our impressions. Why, then, should we conceive of such a mystic unknowable and objectless Something? It is completely unnecessary. If we analyze the world in a purely empiric manner, and discard, in a strictly scientific way, every hypothesis, we find no such dualism in the world. The entire world consists of psychic impressions, and nothing else is to be found anywhere.

We must accustom ourselves to this incontrovertible fact, which is becoming to-day more and more widespread. The world, then, appears completely uniform, and many of the difficulties disappear. There is not a division into material and psychic, parallel to one another. Here all is unity, a mighty sum of psychic impressions and their complexes; that is, the Psyche, that is, the world, and all scientific investigation consists in the analysis of its contents. The limits between science and psychology also disappear. We pursue the same method in both sciences; we analyze psychic complexes and lay down general laws; we do the same in physiology. As a special science it is thus limited to a special part of the entire corporeal world, to the complex of impressions, which we as organisms feel. Thus physiology is a part of psychology, as well as of natural science. For in the broadest sense psychology includes all science.

I am at the end. Many wanderers travel far away, seeking for truth. They spread themselves toward north and south, toward east and toward west. They wander through the world on painful, intricate paths. At the end, however, they all meet at their goal.

Thus it is with knowledge; however far they may be separated from one another, however specialized and differentiated they may be, as they penetrate more deeply, all sciences approach one another more and more closely. Finally, however, all the paths of investigation end, as their last goal, in the one great realm of psychology.

PROBLEMS OF PHYSIOLOGY OF THE PRESENT TIME

BY WILLIAM HENRY HOWELL

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Most of the masters in physiology have attempted in one way or another to lay before their fellow craftsmen their ideas concerning the right methods to be used in physiology, its natural boundaries, and its future development. We read these utterances sometimes with admiration, sometimes with doubt, but always with interest, and also, alas, with disappointment. For it has not been given to any of our saints or prophets to pierce very far into the uncertain future, and one seeks in vain for a fundamental thought or principle which shall illuminate the mystery of life. Our greatest men have, in fact, been wise enough to teach us by example rather than by precept; the chief lesson that one may learn from their lives and writings is that we must continue to investigate, to observe, and to experiment, and that in this way only can sure progress be made toward the goal of which we all dream. The time seems not yet ripe for the master-mind to gather the scattered data and mold them into great generalizations or laws such as have been achieved in other sciences. We must, perhaps, admit that the philosophical basis of physiology, its general principles and quantitative laws, have been borrowed in large part from other departments, and that the subject has not as yet fully repaid this indebtedness by contributions derived solely from its own resources. We have no names to which science as a whole owes as much as it does to Galileo, Lavoisier, Newton, Mayer and Joule, Darwin or Pasteur,[1] and since we may claim that our greatest physiologists rank with the first intellects of their age, their failure to penetrate farther into the causation of vital phenomena must be attributed to the intrinsic difficulties and complexity which the subject offers to the human mind. None of us can change this condition, and those who desire to forecast the future must be content, therefore, to view the subject from the standpoint of past experience and the

[1] While two of the names quoted have a right to be classed among physiologists (Lavoisier and Mayer), the contributions made by them which have been so fundamental to all sciences were in the departments of chemistry and physics.

history of other sciences whose field of work has presented apparently less formidable difficulties.

In what may be termed the golden period of physiology, that is, the latter two thirds of the nineteenth century, the period during which the subject became established definitively as an experimental science, the rich and abundant harvest of facts gathered by the first workers who adopted exclusively experimental methods awoke enthusiasm and brightest anticipations. The workers in physiology were animated by a confident belief that their science was on the highroad to a successful solution of the nature and properties of living matter. Now, however, at the beginning of the twentieth century, one hears frequently the voice of dissatisfaction and criticism. Although the workers are more numerous, and the methods and appliances are more complete, the harvest of facts is not so rich nor so significant. Therefore to many it would seem that the methods used are at fault; there is need at least for a new point of view. It requires but little reflection to become convinced that some of the implied or expressed criticism directed toward recent work in physiology is unjust and is founded upon a misconception of its true nature and development. I refer particularly to the belief so frequently expressed that much of the current investigation in physiology is sterile as regards its immediate applicability to practical medicine, and the further statement that the subject itself has become isolated in a measure from the other biological sciences.[1] I do not contest the accuracy of these statements, but both results must be regarded as a necessary outcome of the normal and healthy development of the science of physiology. The general history of physiology is known to us all; it is not necessary to enter into details. It arose out of medicine and developed in intimate relations with the study of anatomy. But even in its earliest history its most significant results were obtained by the use of the experimental method, and in the nineteenth century its separation from the purely observational sciences was clearly recognized. The establishment of physiology as an experimental science is usually attributed to Johannes Müller and his pupils or their contemporaries who fell under his influence. But as I read its history, its modern characteristics, whether for good or for evil, owe their origin as much to the French as to the German school. Johannes Müller himself was not preëminent as an experimenter, — he made use of anatomical rather than physiological methods; but his contemporary Magendie was a typical modern physiologist, and whatever may have been the extent of his personal influence during life, there can be no question that his methods of work and his points of view are the ones that were subsequently

[1] Meltzer, *Vitalism and Mechanism in Biology and Medicine*, *Science*, vol. XIX, p. 18, 1904. Verworn, *Einleitung*, *Zeitschrift für Allgemeine Physiologie*, I, p. 1, 1902.

adopted in physiology. I am not concerned at present, however, with the attempt to estimate justly the relative influence of these great men and their pupils; the simple point that I wish to insist upon is that they established physiology as an experimental science, and pointed out that its most intimate relationship must be with the other experimental sciences of physics and chemistry. Physiology, said Bernard, is not a natural but an experimental science, and most recent writers have defined the subject as consisting essentially of the physics and chemistry of living matter. The two results spoken of above have followed as an inevitable outcome of this course of development. As an independent science, with specific problems of its own, physiology has naturally loosened its connections with the art of medicine. Formerly one of the handmaids of the noble art, it has been freed in a measure from this servitude, and although its results must always be of the greatest importance to the scientific side of medicine, it can no longer be expected to devote itself mainly to the immediate needs of the physician. The practical problems of medicine that can be studied by physiological methods have been undertaken less and less frequently by the physiologist proper; they have fallen to the hands of the pathologist and the clinician. Physiology does its part in this work by giving to such men the needful technique and training which have been developed by the study of its own problems, and the results obtained redound no less to the credit of physiology because the investigator concerned happens to be classified as a pathologist or clinician. All of the sciences are characterized by this mutual helpfulness; the methods and standpoints developed in one frequently give essential aid to the workers in a related science; and the full outcome of the labors of the narrow specialist cannot be justly estimated by the immediate results in his own department. The physiologist proper, the specialist in physiology, must devote himself to the peculiar problems of his own subject. It cannot be otherwise, for who else is to attempt the solution of these problems? The practical interests of such work to medicine may seem to be remote, but it is hardly necessary to repeat the often-quoted injunction, founded upon past experience, that the solution of a special problem of a fundamental nature carries with it in the long run the most important practical results. The state of affairs in physiology is exactly similar to what has long been recognized as proper and natural in chemistry and physics. The chemical problems of practical medicine are not solved by the chemist, scarcely indeed by the physiological chemist. But those who undertake these problems avail themselves to the fullest of the knowledge and methods of chemistry, and without this aid their work would be impossible. In the same way physiology will continually aid in the immediate practical work of medicine, although those who designate themselves as physiologists may less and less frequently give their own hands to such work. We who are physiologists should not be lukewarm nor too critical in our attitude toward the work of the specialist. Those who undertake the solution of the problems of medicine find a large and sympathetic audience; their work wins quick recognition, and oftentimes substantial rewards; while those who attempt the more special and peculiar work of the science of physiology are not likely to attract the attention or the interest of physicians; they must look to their colleagues for encouragement and recognition. What has happened to physiology in this matter of its relation to medicine will eventually be true of the other medical sciences. The tendency is already well developed in the subject of anatomy. The specialist in this subject is no longer interested chiefly in the surgical or medical bearing of his problems; he has questions of his own that look toward the understanding of the great laws of growth and development. Medicine should not wish to keep its children forever tied to its own apron-strings. In proportion as they develop normally and healthfully, they must look forward to an independent existence, and the great mother doubtless will find most honor and help from her offspring as they reach their maturity and contribute to her support otherwise than by immediate hand-service.

It has been inevitable also that the development of physiology as an experimental science should cause it to grow away from the other biological sciences. Anatomy and the morphological side of botany and zoölogy are observational sciences, and their methods vary widely from those employed in physiology. It is still true, of course, that purely anatomical work may furnish important data for physiological conclusions, for instance, in the physiology of the nervous system; yet the tendency of physiology is and has been to depart from such methods, and there has become apparent an increasing lack of sympathy, a lessening of mutual understanding of each other's work between the anatomist and the physiologist. We cannot expect the old relationship to be renewed by a return of physiology to its ancient methods. On the contrary, if there is to be a restoration of the former close union, the advance must come from the side of anatomy. Many of the problems of this latter science will eventually call for the test of experiment, and even now an increasing number of its workers are occupying, as it were, a middle ground between the two subjects, — deriving their problems from the side of anatomy and their methods from the side of physiology. Through the influence of this band of workers it is possible that the two sciences may be brought more closely into touch with each other than has been the case for the last few decades. But while the bond between physiologist and biologist has been less cordial than in former years physiology has found a compensation in the ever-increasing intimacy of its relationships with physics and chemistry. The physiologist looks more and more to chemistry, physics, and physical chemistry for suggestions and methods. How can it be otherwise, if the current statement be true that physiology in the long run has to explain the physics and chemistry of living matter? The truth of this point of view will be apparent to any one who will trace the development of physiology, and it is brought forcibly to the mind of every teacher of the subject when he attempts to direct the training of one who looks forward to a career as a specialist in physiology. I believe that every physiologist feels that the chief preparatory training in his subject should consist in a thorough grounding in physics and in chemistry. If many of the results of recent physiological investigations have not been as decisive as we would wish, is it not probable, nay, almost certain, that the fault lies not in the nature of the problems investigated, nor altogether in the character of the experimental methods employed, but in the inadequate training of the workers? If our investigators were better equipped in the matter of technical training, there would perhaps be less cause for complaint on the score of results, for in physiology, as in the other experimental sciences, the number of problems that may be studied by known methods is very large, one might almost say indefinitely large. We need in physiology not only the great experimenters like Ludwig and Bernard, men with an inborn spirit of curiosity and a talent for experimental inquiry, but also a large number of productive investigators whose capacity may be of a lower order, but whose training shall be complete enough to insure the acquisition of exact and positive results.

If, as I believe, every one will admit the correctness of the facts stated above regarding the tendency of modern physiology to imitate closely the methods used in physical and chemical investigations, the only point to be considered in this connection is whether or not this tendency is premature. Is physiology, in fact, in a sufficiently developed state to employ the methods of the exact sciences? After all, most of the criticism regarding current physiological investigation seems to carry with it the implication that in great part at least the subject as yet is not prepared for the quantitative methods of the other experimental sciences. In considering this point much depends necessarily upon the meaning one gives to the term physical and chemical methods. If we restrict this term to purely physical or chemical studies of living matter in the cell or in the organism, the contention of those who are dissatisfied with the results of recent work is more readily understood, although, in my opinion, far from being justified. Dealing with a substance whose composition is very complex and unstable, and whose structure is not known, it is apparent that rapid progress cannot be expected and exact results cannot often be obtained even by the employment of accurate methods of research. Such work demands, as Ludwig expressed it, that we shall explain each phenomenon as a function of the conditions producing it, or, to use Mach's phraseology, as a function of those variables upon which it depends. It is necessary in such experiments that one condition or set of conditions be kept constant while another is varied in a known way. While this end is often attained in the study of the properties of dead matter, it seems entirely obvious that the complex and unstable living matter should offer much greater difficulty, and that the results obtained should be much less definite and conclusive. Hence the numerous investigations in physiology that lead to diverse and inconstant conclusions. Hence also the error into which falls the over-sanguine physiologist who imagines that he can borrow his method from physics or chemistry and apply it forthwith to the successful study of the properties of living matter. Every one must grant that this kind of work represents the highest ideal of physiological investigation, an ideal toward which the science should endeavor to develop; but judging solely by the results obtained hitherto, one may be forced to admit that the acquisition of positive knowledge by these methods has been slow and uncertain. Such relatively simple problems as the elasticity of the living tissues, the hydrodynamics of the blood-flow, the electrical phenomena of the functional nerve-fibre, the chemical changes of the foodstuffs during digestion and absorption, the chemical changes of respiration and secretion, are still the subjects of apparently endless controversies. Few of the problems of this character that occupied the attenton of our predecessors fifty years ago have been solved satisfactorily. In each generation certain conclusions are accepted and taught, but we are all aware how constantly our views are undergoing change, and how few are the facts that we may consider as definitively demonstrated. The writers of text-books are obliged to prepare frequent new editions not only for the purpose of adding new material, but of correcting the old. In fact, in respect to the exact methods of research, the state of physiology is not greatly different from that of physics or chemistry a century ago. Doubtless much of the work done by these methods is poorly done, or at least leads to no positive conclusions, owing to the intrinsic difficulties of the subject. But granting all this, it seems to me nevertheless that in this direction lies the path of greatest honor for those whose capacity and training mark them as leaders in the subject. We cannot seriously criticise this kind of work without surrendering all hope of the future of physiology. We can only justly criticise the lack of judgment in those who undertake it without sufficient preparatory training or knowledge of the subject.

If, on the other hand, by physical and chemical methods we understand the experimental method, whatever may be the character of its technique, then the question suggested above becomes relatively simple. This, I believe, is the standpoint assumed by the founders of modern physiology, and this is the truth which they wished to emphasize when they claimed that physiology is essentially an experimental science which must develop along lines similar to those worked out in physics and chemistry. When Magendie completed the demonstration of the division of function between the anterior and the posterior roots of the spinal nerves, a distinction that had been assumed by Bell on anatomical grounds, he used the chemical and physical method; he stimulated each root, and thus arrived at a positive conclusion which could never have been reached except by the employment of the experimental method. And those observers like Langley, who in our own day are slowly unraveling the physiological mechanism of the so-called sympathetic or autonomic nervous system and are using experimental stimulation at every stage of the work, are also in this sense employing the physical and chemical method. From this point of view there is no room for criticism regarding the progress, past or future, of the science of physiology. Most of our advance in knowledge has been due to direct experimental inquiry, and the opportunities for further satisfactory work of the same character are lacking only to those who fail in the zeal or talent requisite to imagine and carry out experimental investigations. A recent writer[1] has said, "He who cannot discover and classify new facts in any branch of natural science after a few weeks, or at most a few months, of industrious work must indeed be ignorant or unskilled." As regards experimental physiology, I cannot agree with this author in the implied simplicity of the task of discovery of new facts. I fancy that the unpublished history of the subject contains records of many investigations which were carried out by observers neither ignorant nor unskilled, but which failed to unearth any new facts. But this much seems to me to be certain, that in physiology at present there is abundant opportunity for every grade of investigation. The subject is not so far advanced that new facts of even the simplest kind are without value. That purely anatomical studies may have a profound influence upon physiological theories is illustrated in the most striking way by the history of the so-called neurone doctrine and by the modified views upon this subject that are beginning to be felt in consequence of the anatomical work of Apáthy, Nissl, Bethe, and others. For physiology, however, it is all-important that the ideas suggested from the anatomical side shall be verified and expanded by the experimental method. Bethe's experimental

[1] Ostwald. *The Relations of Biology and the Neighboring Sciences*, University of California Publications, *Physiology*, I, p. 11, 1903.

researches upon the degeneration and regeneration of peripheral nerve-fibers have added greatly to the significance of his anatomical work, and will insure the recognition of the importance of the newer ideas concerning the physiological mechanisms of the nervous system. While I agree most heartily with Verworn [1] that physiology should claim "vollständige Freiheit in der Wahl des Objekts und in der Wahl der Methoden," I find it necessary to supplement this demand by the restriction that the methods, to be physiological, must be experimental. This peculiarity constitutes the shibboleth that serves to distinguish the physiologist from his biological comrades. So long as any physiologist answers to this designation, he should be recognized as a worthy member of our guild. The tendency sometimes exhibited by our most active and prominent workers, to magnify the importance of their own, perhaps newer, methods, by contemptuous or despairing criticism of the methods employed by other workers, seems to me not only ungenerous and unjustifiable, but even positively injurious to the advancement of our science. There is opportunity for important results from all good methods whether old or new, and he whose training or opportunities enable him to do his best work along well-established lines need not be discouraged or diverted in his labors because newer modes are the sensation of the hour. Our greatest teachers have been characterized always by a large-minded sympathy for work of all kinds so long as it is well conceived and well executed.

In all the biological sciences there is an opportunity for physiological work. Hypotheses based upon anatomical facts call for the test of experiment, and the methods that suffice in the beginning may be relatively simple, so that little or no technical training is required for the work so far as the experimental side is concerned. The experimental zoölogist has entered upon such a field. For no good reason he has selected this designation, which seems to suggest the formation of a new specialty. As a matter of fact, experimental work upon animals is necessarily physiological, and the experimental zoölogist must look for his methods and implements to the science of physiology. Work of this kind has all the fascinations of pioneer life; it holds out the possibility of rich discovery, of unexpected finds, and will doubtless attract from physiology and from anatomy the adventurous spirits with large ideas, together with many who are simply dissatisfied with conditions as they are. I cannot, however, sympathize with those who, stirred by the results already reported, seem to feel that all of the energy and ability of our subject should be diverted to this kind of work. On the contrary, however important and attractive this work may be, it is

[1] *Loc. cit.*

distinctly not the best field for the trained specialist in physiology. There is a large domain discovered by the pioneers of other times which needs development. Crude methods will not suffice for this work, and it constitutes the special field for the best-trained artisans in physiology. This most difficult and most fundamental work must be accomplished through the agency of the exact methods of physics and chemistry, and if those who have the requisite training are devoting themselves energetically to this duty, those of us who may lack the ability or special training for such complex undertakings should not be too critical of the results. In the nature of things the work of the pioneer is likely to bring greater glory and recognition to those who make a success of it, but the regions he opens must be subsequently explored and developed. Those who do this latter work are the ones who really determine the importance of each new discovery; they are the ones who ascertain for us whether it is a barren country that has been opened up, or one rich in the possibilities of wealth. This, as I see it, is the kind of work in which the great body of physiologists is actually engaged at present, and it is a kind of work in which the technical methods of physics and chemistry must be of increasing importance.

But whether physiological work is directed along purely physical or chemical lines, or is, to use a current designation, biological in character, so long as its experimental side is emphasized, it is pure physiology, and must, if pursued with energy and ability, contribute to the advancement of our science. This has been the line of development of modern physiology from the time when its founders first pointed out the inadequacy of observational methods and unsupported speculative reasoning. Those who were responsible for giving it this direction of growth felt that its future was thereby assured. "La physiologie," said Bernard,[1] "définitivement engagée dans la voie expérimentale, n'a plus qu'à poursuivre sa marche." For a long time we have been advancing along this path, and it is only necessary to look back to realize the great progress that has been made. When we look forward, however, difficulties present themselves that have made some physiologists doubt whether after all the experimental way will lead us to the end that the science has in mind. The apparently insuperable obstacles continually obtruding themselves always alarm unduly some of our leaders. Fifteen years ago a well-known physiologist, who has himself done much valuable experimental work, exclaimed that our present methods of investigation had reached their limit.[2] "The smallest cell exhibits all the mysteries of life, and our present methods of

[1] Bernard, *De la physiologie générale*, Preface, Paris, 1872.

[2] Bunge, *Physiological and Pathological Chemistry*, Introduction, English translation, London, 1890.

its investigation have reached their limit." But in the brief period that has elapsed since that complaint was made, many additions of striking importance have been made to our knowledge, "with the help of chemistry, physics, and anatomy alone." Since that time the discovery of internal secretions has opened a new field of experimental work; the methods of physical chemistry have found a fruitful application in the problems of secretion and absorption; physiological chemistry has steadily added to our knowledge of the composition of the body; our conceptions of the influence and extent of the action of enzymes has been greatly broadened, and the whole subject of so-called biological reactions, as illustrated by the acquisition of immunity toward foreign substances, has been added to our means of research.

Long ago Borelli and his followers, the iatro-physicists and iatro-chemists, had rightly conceived the method by means of which the problems of physiology should be approached, and if in the eighteenth century the workers in this subject became discouraged and forsook the narrow path of physio-chemical methods and explanations for the broad and easy road of "baseless and senseless hypotheses," [1] who can doubt that the progress of physiology was thereby delayed? Whatever may seem to be the difficulties ahead, however inadequate our methods may appear, the history of physiology, like that of the other experimental sciences, teaches us in the clearest possible way that if we follow steadfastly the advice of our greatest teachers and continue to experiment, to try, new methods will be developed continually which will prove adequate to the fruitful investigation of the seemingly impossible problems that confront us. We have many examples in our own subject of the unwisdom of crying *ignorabimus*. Take the instance of the velocity of the nerve impulse. The greatest living master of physiology, impressed by the idea that the action of the nerve must depend upon the movement of an imponderable material propagated with a velocity comparable to that of light, had declared that it was hopeless to think of arriving at an experimental determination of this velocity within the short distance offered by the animal body. Yet a few years afterward Du Bois Reymond discovered the electrical phenomena of the stimulated nerve, and reasoning from this fact, Helmholtz was led to his beautiful and simple experiments, by means of which the velocity of the nerve impulse was accurately measured. Müller's surrender of the problem was due to a false assumption, and without doubt we or our descendants will find that many of the questions that seem to us beyond the limit of experimental study will be made accessible to investigation by the discovery of new facts and methods. To judge from the past, the great-

[1] Reil, *Archiv für die Physiologie*, vol. I, p. 4, 1796.

est danger and mistake lies always in that hopeless attitude of mind which assumes that what is impossible now to our methods and to our limited vision will remain so forever. I cannot myself see any reason why the physiologist should be despondent of the future, nor why he should depart in any way from the rule laid down by Harvey, "to search out and study the secrets of nature by way of experiment." [1] Those who criticise existing tendencies and methods, and speak vaguely of a better way, have nothing definite to offer, except a return to the barren and disastrous method of speculation by way of the "inner sense." [2]

There are certain large problems in biology which, by definition at least, belong to physiology, but which as a matter of fact do not at present form a subject of investigation by physiologists. Such, for instance, are the great questions of development and heredity, and the varied and important reactions between the organism and its environment included under the term ecology, or bionomics. The course of development in biology has been such that in recent years these questions have fallen mainly into the hands of the morphologists. But the methods employed by the morphologists in their investigations tend to become more and more experimental, and we may infer that the workers who devote themselves to these problems will be compelled to have recourse more and more to the technical methods of physiology. It is therefore a fair question as to whether or not it is desirable that the specialist in physiology should give his attention to work of this character. Burdon-Sanderson, in an address before the British Association for the Advancement of Science, 1893,[3] took the ground that the field of physiology proper, as determined by the course of development, lies altogether in the province of what he calls the internal relations of the organism, that is, "the action of the parts or organs in their relations to each other." This definition is at least an approximately accurate statement of the scope of physiology as it has existed during the past two or three generations. I say approximately accurate, because as a matter of fact some recognized physiological work has concerned itself with the reactions between the organism and its environment, such work, for instance, as the effect of external temperature upon heat production, or the effects of altitude upon the elements of the blood. Still the reaction to the environment has been studied by the physiologist only in so far as the adaptation can be detected at once or within a relatively short period of time. Those reactions that are detectible only or mainly in the progeny have been left very

[1] Quoted from Pye-Smith, Harveian Oration, *Nature*, vol. XIX, 1893.
[2] Bunge, *loc. cit.*
[3] *Nature*, vol. XIX, 1893.

properly to those sciences whose dominant method is that of observation and comparison. In this regard the history of physiology offers an analogy to that of physics. Most of the problems of astronomy and geology are in a wide sense physical problems, but in the division of labor made necessary by the extent of the field to be cultivated, the specialist in physics has limited himself to the study of the properties of inanimate matter so far as they can be approached by the methods of laboratory experiment. The wider relations of this matter to the cosmical processes throughout the visible universe, and its transformations during long periods of time, have formed the subject-matter for independent although related sciences. The astronomer or geologist makes much use of physical knowledge and physical methods, but his subject is large enough to form an independent department of science. A similar division of labor has been followed in the sciences that deal with animate nature, and the part that has fallen to the physiologist is mainly the experimental laboratory study of the properties of living matter. It seems proper, and indeed necessary, that the broader ecological problems should form an independent science which will need specialists of its own. Work of this kind cannot be regarded as lying within the province of the specialist in physiology, although without doubt the development of the physiological sides of the subject will be made largely through methods and technique borrowed or adapted from physiology, and on the other hand the results obtained from ecological work will doubtless exert a reflex influence upon the methods and especially the theories of physiology.

The matter stands otherwise, however, in regard to the deeply interesting and important facts of embryological development. The laws of growth and senescence, the secrets of fertilization and heredity, must be studied in the long run by the physiologist; they are intrinsically physiological problems and must yield at last to the experimental methods of the laboratory. These questions have been studied heretofore chiefly by anatomical methods; but this is the natural order of development. The anatomical side is the simpler; it precedes and serves as a basis for physiological investigation, as the renaissance of anatomy in the sixteenth century formed the logical precursor of a similar awakening in physiology in the seventeenth century. The anatomist has been forced, so to speak, to take up first the problems of development, but of necessity the need for experimental work has soon made itself felt. The results that have been obtained by the use of the simple but ingenious experiments so far employed have been most suggestive, and indicate clearly that a promising future awaits the further extension of this method. If for a time longer such work shall be done mainly by those whose training has been received in the observational sciences, it seems inevitable that the specialist in physiology must also enter the field. Chemical and physical methods are clearly adapted to the study of these problems, for in the end we expect to find the scientific explanation of growth and development in the physical and chemical properties of living matter. The subject is as truly a part of physiology as the processes of secretion and nutrition. In the current literature upon the subject there is at present a freedom in the formation of hypotheses and a reliance upon the virtues of the syllogism which tend to bring it into sympathetic relations with philosophy rather than with physiology. But as the store of observed and demonstrable data is increased, the boundary-line between the probable and the improbable will be more sharply drawn, and more objective methods and less ambiguous theories will mark the development of the subject along experimental lines.

In the strictly physiological literature of the past century, a characteristic feature has been the absence of philosophical speculation. Although the physiologists have been concerned most directly with the problems of life, they, of all the biological family, have been least productive in the philosophical discussions that have prevailed during this period. Those who were most conspicuous in laying the foundation of our exact knowledge followed upon an age of free speculation, and therefore, as it were by protest against this tendency, devoted themselves to an empirical study of the subject, following the admonition of Harvey mentioned above; of Hunter, whose advice was, "Don't think, try;" and of Magendie, whose guiding principle of work was similarly expressed.

At the present time there are indications that the workers in physiology are dissatisfied with this cautious attitude. There seems to be a reaction against the purely empirical procedure, and a demand for the discussion of the underlying philosophical principles. This tendency, in fact, has seemed to affect all of the experimental sciences. "All sciences," says Ostwald,[1] "are tending to be philosophical;" and he and others see in this fact an indication of the approach of an era of synthesis in science, a beginning of the unification of all the widely separated specialties toward a common end. Others will perhaps view this tendency with alarm, and imagine that history is repeating itself; that after a century of objective experimentation the restless mind of man is reverting to the speculative methods of the eighteenth century and attempting after the manner of other days to reach by a shorter path the final goal of an understanding of the mysteries of the universe. Truly, when one examines the results of this recent tendency, he

[1] *Loc. cit.*

finds in them but little to encourage his hopes of a more rapid advance in knowledge. While many protest against the inadequacy of our present methods, the progress that is actually being made is accomplished, as formerly, by those who adhere to the tried method of experimenting continually in every direction. So far as I can see, it is still the duty of the physiologist to insist upon the necessity and value of empirical work. What we need is not so much philosophical theories as new experimental methods, and these will be discovered only by those who, trained in the technique of the subject, are continually attempting to modify and improve existing methods. Physiology needs a Pasteur rather than a Descartes. It is possible that the sciences of physics and chemistry, being so much farther advanced than that of physiology, may feel acutely the need of reconstructing their philosophical basis in order that their working hypotheses may better adapt themselves to future experimental work, but in physiology the guiding principles which we have received from these sciences still hold out richest possibilities of results, and we have not within the limits of our own subject reached that degree of development which calls for a fundamental change in methods or theory. While deprecating, therefore, in the strongest possible way any effort to minimize the importance of the experimental work as now carried on in physiology, it seems to me, nevertheless, quite evident that some value must be given also to the character of the general philosophical idea upon which this work is based. The purely agnostic point of view is suited, perhaps, to individual minds; and where our ignorance is so great the empirical attitude is doubtless the most modest, and theoretically the most justifiable. But human nature is such that an entirely neutral and judicial standpoint fails to arouse in it much enthusiasm or strenuous endeavor. In science we need enthusiasm, for much work is to be done, and scientists as a body, like their fellow mortals, are not content to hold themselves aloof from speculations regarding the final object and significance of their labors. The nature of the underlying philosophical belief has always had an important influence upon the extent and character of scientific work, and we must take this factor into our reckoning in any attempt to estimate the conditions that contribute to the advance or to the retrogression of science.

Toward the middle of the nineteenth century magnificent work in physiology was being done in Germany and in France. The methods that were employed by Flourens, Magendie, and Bernard were as productive and as modern as those used by their contemporaries in Germany, but the influence of the latter school was seemingly more widespread, if we may judge this influence by the effect upon the entire body of investigators in physiology. Recent historians,[1] outside of France, trace the modern revival chiefly to the German school, to the work and the influence of Du Bois Reymond, Ludwig, Helmholtz, Brücke, *et al.* It has seemed to me that one reason for the seeming neglect of the equally important work of the French school lies in the fact that the leaders in the German school were animated by a philosophical principle whose influence not only guided their own work, as it did, indeed, that of the French physiologists, but which was so emphasized and displayed before the eyes of men that it kindled enthusiasm and attracted recruits from all lands to the army of investigators in physiology. The flag under which they marched bore the motto of mechanism, and its followers were animated by the hope that physico-chemical and anatomical methods applied to the experimental study of the properties of living matter would soon bring these mysteries under the control of science. So rapidly indeed were results accumulated in the beginning that the over-sanguine believed the end nearly in sight, and the hope was entertained by not a few that we should soon understand the structure of living matter, and perhaps be able to manufacture it with our own hands. We realize now that this hope was premature. We know much more than our predecessors at the beginning of the nineteenth century; the science has marched onward at a rapid rate; but what seemed to be the end of the forest is only a small clearing, an open space, and in front of us still lies an apparently pathless wilderness. Naturally, therefore, the question has arisen as to whether or not we are following the right route; there has been a more or less general revival of the old discussions regarding mechanism and vitalism. On the basis of the knowledge and experience obtained by a century of work, there is a disposition to orient the subject anew regarding these guiding principles of investigation.

Recent writers have recognized various degrees or kinds of vitalism, the mechanical and psychical, the natural and transcendental, and the neo-vitalist, as distinguished from the vitalist of the eighteenth century. Leaving aside ultimate views as to idealism or materialism which can scarcely be supposed to exert any direct influence on scientific work, it seems to me that the vitalist in physiology now is what he has always been, one who believes that there is a something peculiar, a *quid proprium*, to use Bernard's expression, inherent in or indissolubly connected with living matter, a something that is different from matter and energy as understood in physics and chemistry, a something, therefore, that does not necessarily manifest itself in accordance with so-called physico-chemical laws. The name that we may give to this something matters but

[1] Tigerstedt, *Zur Psychologie der naturwissenschaftlichen Forschung*, Helsingfors, 1902; Burdon-Sanderson, *loc. cit.*

little; we may call it soul, animal spirits, vital principle or force, ether, nervous fluid, inner sense, consciousness or psyche, but *plus c'est changé, plus c'est la même chose.* We may differ as to whether this something is connected with living matter in all its forms or whether its manifestations are limited to the nervous tissues, but if we admit its existence as a causal factor in any of the phenomena of life, then it seems to me that we adopt the standpoint of vitalism, and the nature of our work as well as our theories will be influenced thereby. The standpoint of the mechanist is simple. He believes that all the properties of living matter are of a chemico-physical nature, that is, properties that are dependent upon the structure and arrangement of the molecules and the eternal characteristics of their constituent parts. The C, H, O, N, S, P, etc., that enter into its composition carry with them their individual properties, and if nothing else is present in living matter, the phenomena exhibited by it must be a resultant of these properties, as the phenomena exhibited by sodium chloride depend upon the combination of the properties of the constituent sodium and chlorine. From this standpoint we may assume that if there is in living matter any recognizable form of energy not hitherto classified, it is intrinsically present in dead matter also, and we may hope to discover its existence by purely physico-chemical methods of investigation, with the probability, indeed, that it will be recognized first by the chemist or the physicist with his more exact methods and more favorable conditions for quantitative analysis. If we are unwilling to adopt this standpoint, then it seems to me that, unless we deem it wiser to assume an entirely agnostic attitude, we are logically forced to take one of two positions. With the older physiologists we may boldly assume the existence in living organisms of a finer stuff intermingled with the so-called matter, a substance that is not matter as we understand that term in science, but which, in combination with matter, gives to living things their distinctive characteristics; or we may assume the existence in the universe of a reality other than matter, with the belief that it is influenced by and exerts an influence upon matter only in the living form, in some such way as the earlier physicists postulated an ether that can be affected by matter only when in a certain state of vibration. If I read them correctly, most modern scientific authorities adopt substantially this latter point of view. The so-called psychical phenomena of life are differentiated from the physical, but at the same time it is admitted that the subjective or psychical manifestations are dependent upon physico-chemical changes in the material substratum. Huxley states the matter with his usual candor and clearness: "It seems to me pretty plain that there is a third thing in the universe, to wit, consciousness, which in the hardness of my head or heart, I cannot see to be matter or force or any conceivable modification of either." It is perhaps a question of terms only as to whether this point of view is properly designated as vitalism. Inasmuch, however, as it assumes a something that can be influenced only by living matter, possibly only by special forms of living matter, and in turn can only act upon living matter, it draws a line between the properties of the animate and the inanimate which represents a real distinction, and those who hold to this point of view or any modification of it can scarcely escape, for want of a better term, the designation of vitalist, even though it is recognized that the reaction between the subjective and the objective world may be governed by laws that are, strictly speaking, as mechanical as those reactions of matter that have been generalized under the laws of physics and chemistry. In this sense I believe that the majority of physiologists belong to the school of vitalists. The methods that they employ and the nomenclature they use are, however, mechanical, because the science recognizes that its ultimate aim is to understand the mechanics of living matter, and that in this way only, if at all, shall we be able to arrive at a conception of the relations of this matter to a reality of a different order. The older physiologists, and some of recent times, have used the conception of vitalism as a convenient and easy means of accounting for many processes which further investigation has shown to be purely mechanical. Experiences of this kind tend to strengthen our belief that most of the unknowns confronting us at present will be analyzed eventually in terms of the conceptions of physics and chemistry; but there is always present in physiology the tendency to assume that what is not clearly or conceivably reducible to the laws of matter and energy must therefore belong to the "irreducible residuum." The nature of this residuum, the connotation of the term vitalism, varies somewhat with each generation.

Bernard, in his lucid and masterly discussion of the phenomena of life, came to the conclusion that the irreducible residuum, to which the laws of chemistry and physics are not and cannot be applicable, is the power of development of the egg. "Car il est clair que cette propriété évolutive de l'œuf, qui produira un mammifère, un oiseau, ou un poisson, n'est ni de la physique ni de la chimie. . . . La force évolutive de l'œuf et des cellules est donc le dernier rempart du vitalisme."[1] In our own day the study of the mechanics of development is actively pursued by many investigators, and I fancy that few modern physiologists are inclined to take a truly vitalistic view of the process. However much the facts of development are beyond the possibility of explanation in terms of our present chemico-physical knowledge, it is clearly conceivable that the

[1] Bernard, *Revue des Deux Mondes*, IX, p. 326, 1875.

observed processes may all be due solely to the material structure of the fertilized ovum acting in accordance with physico-chemical laws, and that, therefore, our present methods of investigation may eventually bring these phenomena within the limits of a scientific explanation. The irreducible residuum recognized to-day, and indeed admitted always by many of the physiologists who are reckoned among the mechanists, is the psychical reaction, the phenomenon of consciousness. However much we may come to know of the physico-chemical processes that give rise to this reaction, it has been asserted by most of the scientific authorities of our time that the psychical side itself is beyond the possible application of the methods of physics and chemistry, a conclusion that, as it seems to me, is tantamount to the admission of the existence of a non-material reality. The study of consciousness has therefore been eliminated from the subject of physiology on the ground that the methods of our science are inapplicable. I fully agree, however, with the timely and courageous statement of Minot [1] that "Consciousness ought to be regarded as a biological phenomenon, which the biologist ought to investigate in order to increase the number of verifiable data concerning it." If for the present this task is confided to the workers in the independent science of psychology, the only successful methods that they can employ are those of observation and experiment, and eventually the latter mode of investigation must become the more important, and the subject must be recognized as destined to come within the province of experimental physiology. To Minot the most important work at present is to be accomplished by an extension of the comparative method to the psychological study of all forms of life, but to the physiologist it would seem that a no less promising although technically more difficult field will be found in neuro-pathology, which holds out hopes that definite variations in the psychical reaction may be connected with distinct alterations in the structure and properties of the material substratum. One can scarcely doubt that the combined labors of the psychologist, biologist, physiologist, and pathologist will eventually accumulate many verifiable data concerning consciousness. We are not able at present, it is true, to form any conception of the nature of the relation between the subjective and the objective, but new facts may alter wonderfully our insight into this mystery, and it is the clear duty of physiology to participate in the work of accumulating all possible data bearing upon this relation. The introspective method alone is insufficient, and we have no alternative but to trust hopefully in the less pretentious method of scientific observation and experiment. We may believe that in this

[1] Minot, *Presidential Address*, American Association for the Advancement of Science, Pittsburgh Meeting, *Science*, XVI, p. 1, 1902.

way a basis will be obtained upon which philosophy may reason, more surely and more successfully than is possible now, concerning the psychical life and its relations to the mechanical phenomena of the universe.

If I may summarize briefly my point of view regarding the present problems of physiology, what I have wished to emphasize is this. The experimental method, physical, chemical, biological, or anatomical is the life and hope of the subject. Its future depends solely upon the steadfast recognition of the necessity and possibilities of this means of research. Every investigator who is anxious to add to the stock of physiological knowledge should experiment ceaselessly by those methods which he is most capable of using, while those who are looking forward to the highest work in physiology should fit themselves by a thorough training in physics or chemistry, since the most difficult and the most fundamental problems in the subject require the use of the methods and modes of thought of these sciences. There must be an outlying division of workers who will keep the subject in touch with practical medicine, and other divisions through which communications will be established with psychology and the morphological sciences; but the flower of the army, the imperial guard, will consist of those who have been disciplined in the methods of physics and chemistry, and who are able to apply this training to the study of the properties of living matter.

SHORT PAPER

Professor E. P. Lyon, of St. Louis University, read a contribution before this Section "On the Theory of Rheotropism in Free Swimming Animals," in which he discussed the orientation of organisms in streams of water, a phenomenon frequently observed, but having received thus far little attention.

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(*Prepared by the courtesy of Professor Oscar Drude*)

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WORKS OF REFERENCE ON THE SECTIONS OF BACTERIOLOGY, ANIMAL MORPHOLOGY, EMBRYOLOGY, COMPARATIVE ANATOMY, HUMAN ANATOMY, AND PHYSIOLOGY

(*Prepared by the courtesy of Professor Henry B. Ward of the University of Nebraska*)

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ADDENDA PAGES

FOR LECTURE NOTES AND MEMORANDA OF COLLATERAL READING