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CONTENTS:

<i>Development of Morphological Conceptions:</i> PROFESSOR JOHN M. COULTER.....	617
<i>The Concepts and Methods of Sociology:</i> PRO- FESSOR FRANKLIN H. GIDDINGS.....	624
<i>Recent Advances in the Analysis of the</i> <i>Earth's Permanent Magnetic Field:</i> DR. L. A. BAUER	634
<i>Scientific Books:—</i>	
<i>Thorndike's Educational Psychology:</i> PRO- FESSOR H. AUSTIN AIKINS. <i>Some Recent</i> <i>Literature on the Stony Corals:</i> DR. T. WAYLAND VAUGHAN	644
<i>Societies and Academies:—</i>	
<i>The New York Academy of Sciences, Sec-</i> <i>tion of Biology:</i> DR. M. A. BIGELOW.....	648
<i>Discussion and Correspondence:—</i>	
<i>The Earliest Mention of Fossil Fishes:</i> DR. C. R. EASTMAN. <i>Paleontologia Uni-</i> <i>versalis:</i> PROFESSOR CHARLES SCHUCHERT. <i>A Proposed Geographic Dictionary:</i> DR. CLEVELAND ABBE, JR. <i>Amœbæ for the</i> <i>Laboratory:</i> DR. A. W. WEYSSE. <i>Do</i> <i>Rhizopods die a Natural Death?</i> PROFESSOR L. C. WOOSTER. <i>Body Temperature:</i> C. F. LANGWORTHY. <i>Mathematics and Meta-</i> <i>physics:</i> PROFESSOR A. HALL.....	648
<i>Special Articles:—</i>	
<i>What is an Electric Current?</i> PROFESSOR FRANCIS E. NIPHER.....	651
<i>Scientific Notes and News.....</i>	652
<i>Educational Notes and News.....</i>	655

DEVELOPMENT OF MORPHOLOGICAL CONCEPTIONS.*

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 zoology 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.

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

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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.

1. 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, 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 remem-

bered 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 simplification of complex structures, is now in its decline.

2. 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 heterosporous. Study of the metamorphoses of plant organs was re-

placed 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 center 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 skilfully, but very seldom do the facts seem to be coordinated. 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 regime. 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 simi-

larity 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 dominated 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.

3. 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 variation, 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, exper-

imental 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

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 entrenches 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 evi-

dent 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. The attempt 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 record 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 can not 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.

JOHN M. COULTER.

THE UNIVERSITY OF CHICAGO.

*THE CONCEPTS AND METHODS OF
SOCIOLOGY.**

To set forth in a brief paper the fundamental conceptions of any modern science is a difficult task. The difficulty increases as we pass from the relatively simple sciences that have to do with inorganic matter,

* An address delivered at the International Congress of Arts and Science, Department of Sociology, September, 1904.