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The American Association for the Advancement of Science:
Morphology as a Dynamic Science: PROFESSOR EDMUND W. SINNOTT ... 61

Obituary:
Stanley R. Benedict: DR. H. D. DAKIN. *Grafton Elliot Smith:* DR. WILLIAM K. GREGORY. *Recent Deaths and Memorials* ... 65

Scientific Events:
The Soil Conservation Service; Research Program of the Food and Drug Administration; The Annual Meeting of the Geological Society of America; The Award of the Perkin Medal of the Society of Chemical Industry ... 69

Scientific Notes and News ... 71

Discussion:
The Distribution of Black Widow Spiders: B. J. KASTON. *The Black Widow Spider in Virginia:* H. A. ALLARD. *The Similarity of Action of Male Hormones and Adrenal Extracts on the Female Bitterling:* PROFESSOR ISRAEL S. KLEINER, ABNER I. WEISMAN and DANIEL I. MISHKIND. *Parthenogenesis in the Grasses:* DR. E. L. STOVER. *Alkalize, Alkalinize and Alkalify:* T. W. DAVIS ... 74

Special Correspondence:
Fourth Annual Tri-State (Illinois, Iowa, Wisconsin) Geological Field Conference: PROFESSOR A. H. SUTTON ... 76

Special Articles:
Built-up Films of Proteins and Their Properties: DR. IRVING LANGMUIR, VINCENT J. SCHAEFER and D. M. WRINCH ... 76

Science News ... 8

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MORPHOLOGY AS A DYNAMIC SCIENCE[1]

By Professor EDMUND W. SINNOTT

BARNARD COLLEGE, COLUMBIA UNIVERSITY

WHEN a science has developed to the level where it can recognize the fundamental problems which confront it, it may be said to have passed from youth to maturity. Long ago the physical sciences were able thus to formulate their objectives, and they have made enviable progress in attaining them. Biology, on the other hand, throughout its history has moved from one major interest to another and has never seemed able to distinguish its fundamental problems from a host of minor ones, or indeed to determine whether or not there exist any strictly biological problems at all. Not many generations ago the naming and classification of the host of plant and animal species was regarded as the chief task of the biologist. This naive attitude was altered by an acceptance of the tremendous fact of evolution, which seemed to make obvious that the central problem of both botany and zoology was to write the entire phylogenetic history of the organic world, a task which commanded the allegiance of the majority of biologists for half a century.

As time went on, however, it came to be realized that the ultimate secret of a living organism will never emerge from the records of its ancestry, no matter how completely these may be deciphered. Physiology is evidently nearer than phylogeny to the ultimate problem. Stimulated by the great advances which the physical sciences had made, the attack through physiology began about a generation ago to attract many new workers and gave every promise of substantial progress. The years have found this promise amply fulfilled in our success in plotting the flow of physical and chemical change of which an organism is the seat, but the results of physiological research have tended

[1] Address of the retiring vice-president and chairman of the Section on Botanical Sciences, American Association for the Advancement of Science, Atlantic City, December 29, 1936.

to emphasize the complexity rather than the simplicity of protoplasm and have entirely failed as yet to solve the elusive problem of what an organism really is. A similar frustration has attended still another line of attack, through the science of genetics. Ever since the rediscovery of the Mendelian principles of heredity, this discipline has been enthusiastically pursued by many students who felt that here, at last, something fundamental in biology had made its appearance. The truly sensational development of the chromosome theory, with its demonstration that the genes are definite physical entities occupying constant positions in the chromosomes, has justified this early enthusiasm; but with their first major objective attained, geneticists are coming to realize that their really basic problem is not the location and transmission of genes but the mechanism by which these control the development of an organism, a question about which our ignorance is almost complete.

Although these attacks on so many widely separated fronts have not yet pierced to the center of the problem of life, they have served to clear away many obstructions and to open the road toward our chief goal, which is now just beginning to appear. Biologists are at present in the position of the early explorers of the mighty mass of the Himalayas. They have pushed in from various directions, seeking the best and most practicable routes. Many of the foothills have been climbed and a few important peaks conquered. The increasing difficulties of the terrain, once underestimated, are now recognized. Still more important, the existence of a central dominating range seems to have been established and glimpses have been gained of the very highest peak itself. The main objective of our labors is at last becoming more clearly defined.

To formulate with anything like assurance a problem which is central and fundamental for all biology, the Mount Everest of our scientific exploration, may still seem to many an act of faith rather than of sight; but within the last few decades, and recently in increasing numbers, many biologists, as well as thinkers who have approached biological problems through the physical sciences and through philosophy, are agreed in emphasizing one particular problem, one general phenomenon of life, as of primary and dominant significance. This may be stated in a word as the problem of *organization*. Living things are well termed *organisms*. The activities of their manifold structures are so integrated and coordinated that a successfully functioning whole individual develops. As to how this is accomplished very little is known. The advances of biological science have been chiefly in quite the other direction, in breaking down the organism into its constituent organs, tissues and cells, into chromosomes and genes, into protein molecules and cellulose chains, into potential differences, axial gradients and morphogenetic fields. But analysis alone, however detailed it may ultimately be made, can never lead to a complete understanding of an organism. Synthesis also is required. What it is that coordinates these various parts and processes so that an organism rather than a chaos results, what synthetic factors there may be which knit the organism together into a functioning unit, are extraordinarily difficult problems. They do not yield readily to the direct and obvious methods of attack which have usually been employed in biology and they tend to become involved in philosophical as well as strictly biological difficulties. It is probably safe to say, however, that the majority of botanists and zoologists to-day would admit that this problem of organization is indeed their ultimate and central concern; and that if the biological sciences have any problem peculiar to themselves and differentiating them from the physical sciences, this is the one.

My purpose in making such an excursion as this into biological fundamentals is to defend the thesis that the solution of our basic problem can be approached more simply and directly through the study of *form* than by any other means; and that morphology, far from being the hopelessly static discipline which some would have us believe, therefore touches so intimately the central problem of biology that it may still be described by Darwin's words, in a famous passage of the "Origin," as the "very soul" of natural history. Let us examine the evidence for this contention.

The correlative mechanisms by which an integrated living individual is maintained are, of course, physiological in character and are doubtless ultimately resolvable into physical and chemical processes; but their investigation from the point of view of physiology alone is usually beset by such difficulties that substantial progress on this front must wait until the necessary experimental technique is much more highly perfected than it is to-day. The coordinating and integrating capacity of protoplasm, however, is displayed not only in those correlations of function which so excite our amazement but also in the more familiar and no less remarkable correlations of growth, operative during the process of development and resulting in the production of those specific and constant shapes of organ and body which are so characteristic of living things. A fertilized egg divides this way and that in such a precise manner that an embryo with two cotyledons, a plumule and a hypocotyl, definite and specific in form, are produced. From a tiny mass of undifferentiated cells at a growing point are developed the primordia of organ after organ in a perfectly regular fashion, and each follows in its enlargement a definite pattern of growth. In all such cases there is manifest in the clearest fashion that coordinating control of which I have spoken. Form is merely the outward and visible expression, fixed in material shape, of that inner organized equilibrium which we are seeking to understand.

A study of organization as thus expressed in form has the very great advantage that it deals with a visible and stable product, readily observed throughout its entire period of development and measurable with relative ease. The dynamic system which underlies this development of form, on the contrary, consists of a series of physical and chemical processes so complex and changing that they are much more difficult to recognize and to measure. Their product, to be sure, is less immediate to our problem than the process which forms it, but product can often be investigated where process can not. We should first examine these more tangible aspects of the phenomenon of organization, using them as a means of penetrating to the more obscure vital activities by which they are underlain.

If it be admitted that our basic problem can thus be approached most simply and directly through the door of morphology, then an investigation of the factors which determine organic form assumes a major place in biological science. That this importance is coming to be generally recognized is evident in the diversity of directions from which developmental problems in plants and animals are now being attacked. Physiology has always regarded correlative development as an integral part of its domain, but in recent years this subject has assumed a steadily growing importance, as witness the intensive researches on hormones, organizers, metabolic gradients and morphogenetic fields. Genetics is now increasingly concerned with an attempt to discover how genes control development and thus produce the traits by which they are recognized. Ecological attack upon the problem of changes in form through environmental factors has been intensified by discoveries in various fields. Even physicists and chemists have been intrigued by developmental problems and have made important contributions toward their solution. This field of investigation—call it experimental morphology, causal morphology or morphogenesis—is thus drawing to itself some of the best thought and skill of the biological sciences and promises soon to assume a position of major interest and activity.

In this diversified attack upon the problem of the causes of the coordinated developmental processes which result in the production of organic form, only a relatively minor part, strangely enough, has been played by those biologists who might have been expected to be more interested in it than any one else—the morphologists themselves. With important exceptions, those botanists and zoologists whose primary concern has been with the form and structure of living things have contented themselves with the static and descriptive aspects of their science rather than with its dynamic and developmental side. The reason for this one-sided emphasis in morphology is evidently a historical one. The form of organisms has always fascinated biologists. Its constancy in each species, its almost infinite diversity and the existence of underlying similarities in form between groups of organisms have persistently demanded an explanation. Long delayed though this was, it seemed at last to have been completely and triumphantly provided by the theory of evolution. What could be more obvious than that all this diversity of form was the result of evolutionary divergence? What more certain than that structural homology was due to common ancestry? Under the tremendous impact of this new idea it was inevitable that students of organic form should regard as their primary task a careful description of the external and internal structure of plants and animals so that by diligent comparison of a wide range of types the evolutionary history of the organic world could be reconstructed. In the period of its greatest expansion morphology thus became preoccupied with phylogeny to the exclusion of almost everything else, and this primary interest has largely persisted to the present time.

Such preoccupation is to be explained not only by the importance of the phylogenetic task itself but by the inherent attractiveness of such problems as these. The piecing together of evidence from many sources, the reconstruction of divergent lines of evolutionary descent within a group of organisms, and the recognition of homologies between apparently diverse structures excites the same sort of interest as does a jig-saw puzzle or a detective story and appeals to the primitive human urge to bring order out of chaos. No one who has ever tried to solve a phylogenetic problem can fail to recognize the peculiar fascination which it possesses for its votaries.

With all these influences at work it is therefore not surprising that the purely descriptive and historical phases of their work have attracted the chief attention of most of those whose major interest is with the study of organic form. The results of this study have been of very great significance in the development of biology, and the writer has no wish to disparage them in any way or to belittle the contribution which they have made and will continue to make toward our understanding of living things. Nevertheless, if the argument developed in the present paper is sound, the dynamic aspect of the problem of form is of far greater ultimate significance than its descriptive side alone. Morphology should concern itself with causes as well as with results, and should not abandon this most promising, though most difficult, part of its territory to be explored by physiology, genetics, biochemistry and other sister sciences whose main interests lie elsewhere. If it is at this spot where the chief treasure is hidden, the cooperation of all is surely to be welcomed in bringing it to light, but those who first staked out a claim here should lead in the search and be sinking the deepest shaft.

To all this it may be objected that names are unimportant; that whether those who attack the dynamic aspect of form call themselves morphologists or cytologists or biophysicists is quite immaterial, for no morphological caste or guild can claim precedence for itself here. Of course this is true, but as a practical matter it should not be forgotten that the material which presents itself to the student of morphogenesis is complex and requires a rather special knowledge on the part of the investigator if he is to be safe from error and waste of effort. An outsider is notoriously prone to make absurd mistakes if he works in a field which is not his own by experience and training, and nowhere is this more true than in problems involving the data of morphology. One who is well trained in this field has a very real advantage in morphogenetic studies.

But the morphologist may object again that by temperament and training he is unfit to undertake problems involving the dynamic side of his subject, since these require an approach through experiment and the methods of the physical sciences, with which he is often unfamiliar and unsympathetic. As he can not thus be of real service here, he may ask, why not leave him in the ivory tower of his phylogenies and his life histories and turn over to the physiologists and their allies, fortified by a little better morphological training, the whole troublesome task of determining the causes of form?

Such a defeatist attitude, it seems to me, is based on the erroneous assumption, often made by both morphologists and non-morphologists, that the only way to attack the problems of morphogenesis is by experiment, involving almost immediately the techniques of the physical sciences. No one, of course, questions the great importance of the experimental method or the desirability of resolving as promptly as possible the problems of development into the simpler ones of physics and chemistry; but as a matter of sober fact, most of these problems are not yet in a position where they can profitably be attacked in this manner at all. Before we can intelligently set up experiments to determine the integrating and coordinating growth processes which control development and produce specific forms, we must first obtain precise descriptive information as to *exactly how development proceeds.* Furthermore, in most cases where as the result of experiment a difference of form or structure has been produced, it is of the utmost importance to analyze in morphological terms the exact changes involved. Long before normal development, or experimentally produced changes in it, can be expressed in physical or chemical terms, they must be expressed in morphological terms. The first step backward from the visible end result of a developmental process toward the ultimate inducing cause—be this gene, hormone or radiation—must be a more refined *description* of this result and of the visible steps which lead up to it. This is obviously a job for the morphologist. An enormous amount of spade-work of this sort needs to be done in almost every morphogenetic problem, for our knowledge of the exact steps in the development of most organs, in terms of cells, tissues and precise visible changes, is still shockingly meager. In our haste to interpret results in ultimate terms we have too often failed to find out exactly what these results really are. The chief service which the descriptive morphologist can do for the experimental morphologist is to provide just this sort of information. No one can do it as well as he. I believe that there is no other task confronting him which is so important.

But it is not only a descriptive knowledge of development as expressed in words that the student of morphogenesis requires. In one important particular the morphologist must change his usual technique if he is to make it serve the dynamic aspect of his science: *he must present his results in quantitative terms.* Only thus can they yield themselves to precise analysis and to interpretation in terms of the physical sciences, and only thus can they serve as a means for the discovery of new facts and relationships. To the scalpel and forceps, the microtome and the microscope, the morphologist must add the ruler and the scale as part of his equipment if he is to make his data serviceable to morphogenetic science.

An example or two will illustrate the essential part which quantitatively descriptive morphology can play in developmental and morphogenetic problems.

The coleoptile of the oat has long been an important organ for the study of the effects of plant hormones on development. Its growth and angle of bending have been measured in many experiments, but not until recently was its developmental history carefully studied in terms of internal structure. Avery and Burkholder have now determined the distribution and duration of cell division within it and have measured the changes in cell size in all its tissues and in all stages from seed germination until it reaches maximum growth. This was a morphological task, but it has provided the necessary basis for any thorough-going analysis of the precise effects of hormones on the development of this organ.

In my own laboratory we have been studying the genetic basis of shape differences in the fruits of the Cucurbitaceae. These characters can be described by the patterns and shape indices of the mature fruits, but such tell only part of the story. It is essential to learn the developmental history of each type if we are to find what the genes actually control here. When length and width are measured at successive stages from ovary primordium to ripe fruit it is found that they grow at different rates, so that the fruit changes in shape somewhat during its development. The relative growth rate is consistently different in different races. In the Hercules club, length grows faster than width, so that the fruit becomes progressively more elongate. In the bottle gourd, on the other hand, width grows faster than length. Within a given race, however, this relationship is so unvarying that it may be expressed by a simple value or constant and thus used to describe very precisely the most important aspect of a fruit-shape difference. This constant relative growth rate segregates in inheritance and seems to be what the genes governing shape primarily control. It thus constitutes an important step into that unknown territory between the gene and the visible shape which this determines. The existence of such a constant relationship as this in the midst of developmental diversity and change could not have been recognized without a careful descriptive study of the entire history of the growing fruit, expressing its results not only in words but in measurements.

Such examples could be multiplied almost indefinitely, and from work with animals as well as with plants. The whole domain of developmental morphology, illuminated by the ideas and view-point of morphogenetic research and attacked by quantitative as well as qualitative methods thus offers a wide field for fruitful investigation. Let no one disparage such studies as "merely descriptive." Description must precede explanation, and in the combined attack on the problem of organization the morphologist should be a leader, not a follower. His is the task of the pioneer entering a wilderness of facts, which must be explored and cleared up before those who follow in his steps can practice their arts of greater refinement and precision.

For the welfare of biology as a whole, therefore, it is my plea that those who have been trained in the rigorous disciplines of morphology may turn in increasing numbers to the more dynamic aspects of their subject. Especially let us hope that those younger botanists and zoologists who choose to devote themselves to the problems of organic form may realize that these can not be set apart as a static compartment of biological thought but must touch and illuminate the whole. May they help to resolve for us this fundamental paradox: that protoplasm, itself liquid, formless and flowing, inevitably builds those formed and coordinated structures of cell, organ and body in which it is housed. If dynamic morphology can come to the center of this problem, it will have brought us close to the ultimate secret of life itself.

OBITUARY

STANLEY R. BENEDICT

THE death of Stanley Rossiter Benedict on the night of December 21 was a grievous shock to his friends and colleagues. He was only fifty-two years of age, and while he had suffered some physical disabilities in recent years he seemed to his friends to be in the prime of useful life until about a week before his untimely end.

Benedict's claims to distinction are of a very substantial order. As professor of biological chemistry in the Cornell University Medical College, he was a teacher of wide repute, who added much to the dignity of a young and growing department, where many workers of both sexes obtained not only knowledge but standards of scientific integrity which served them well in later life. His collaborators make up a lengthy list, and in addition to the younger workers his long association with Emil Osterberg, who survives him, is happily commemorated in many joint publications. Like all generous men Benedict was only intensely pleased with the successes that came to his former pupils. His early training had been in part at New Haven, and in most respects he was a true disciple of the Chittenden-Mendel tradition of physiological or metabolic chemistry. He possessed in addition masterly skill in analytical chemistry, a sound appreciation of physiology and considerable knowledge and ready understanding of the problems of structure that organic chemistry was presenting to the developing science of biochemistry. His attitude to the purely physical side of his subject may probably be described as receptive and sympathetic rather than enthusiastic.

His skill as an analyst can only be compared with that of Folin, with whom it must be confessed he was frequently in spirited argument, which only served to cement the underlying friendship of the two men, who really had much in common. Benedict's researches on the estimation of sugars, creatine, creatinine, purines, uric acid, phenols, sulfur, glutathione, ergothioneine and many other substances, by both macro and micro methods have become part of every biochemist's training. But he was not content with analysis for its own