SURVEY OF BIOLOGICAL PROGRESS

G. S. Jr. Avery

VOLUME III

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PREFACE

This series of volumes aims to present to biologists and other interested scientific readers a series of reviews that will be comprehensive in scope and provide perspective in viewing the growth of the biological sciences. The first two volumes, under the able editorship of George S. Avery, Jr., touched on teaching problems in present-day biology. Principles common to all biology were examined in areas such as those dealing with the nature of genes and of gene action, the effects of radiation on biological systems, and the fine structure of protoplasm. New developments of methodology—tracer methods, histochemical methods, and methods of breeding disease-resistant vegetables—were described. Broad aspects of growth and development, as seen in plant morphogenesis, plant growth hormones, the physiology of plant reproduction, vertebrate development, and the control of hormones over sex differentiation in animals, were prominently considered. Other reviews had to do with the bearing of nutritional factors on reproduction and of environmental factors on the vitamin content of plants; with ecological studies of populations and biological oceanography; and with virus tumors. In succeeding volumes it is hoped that an even broader scope may be encompassed, even greater perspective afforded.

At the present time, in historical treatments of biology, there is a curious gap between the chronological point at which historians almost universally conclude their accounts, at about the opening of the present century, and the point at which a young student of the field finds himself at the beginning of his specialized work. The concepts now current and the methodology now applied are often separated by a chasm of no little breadth and depth from the "classical" concepts and methods of biology at the turn of the century. Somehow this chasm must be bridged, if our student is to perceive his whereabouts and to handle his conceptual armamentarium with skill. To bridge the chasm at numerous points will be the undertaking of a series of articles, to appear in successive volumes, each in one major experimental branch of biology. The first of these is the opening review in the present volume, an article by Jane Oppenheimer, which ably traces the growth and transformation of significant embryological concepts in the twentieth century.

Another signal need for the general student is the analysis of trends in various fields of biology currently undergoing strong modifications in viewpoint or experiencing a reawakening of interest in long-dormant areas. The more descriptive and taxonomic fields in particular are today sharing a revivification, as the implications of evolutionary and ecological studies make themselves felt in the "new systematics." Inasmuch as the analysis of variation is basic in all biological studies and the problems of classification enter into every choice and use of biological material, no one should fail to profit from the very comprehensive and illuminating treatment of trends in systematic botany, prepared by David D. Keck. It may be safely said that no review of this sort has been previously available, and it should prove to be invaluable. The editor hopes to follow up this review of trends in systematic botany with one in some future volume, on trends in systematic zoology. Meantime, one particular aspect of the evolutionary and systematic approach to the study of animals is provided in the review by M. J. D. White of chromosomal evolution and its relation to polymorphism and to speciation in the animal kingdom.

Since the Second World War the study of animal behavior, particularly in Europe, has been reinvigorated. Much of the newer study of behavior is firmly based on an experimental approach, over and above the descriptive and analytical methods of earlier times. It is gratifying to be able to present a review in which insect behavior—which is by no means limited to the highly popularized studies of von Frisch and others on bee communication—is placed in the appropriate physiological context. Chemoreception is surely quite as significant as vision in orienting insect behavior, whether in foodgetting or in mating. V. G. Dethier's review should do much to sharpen the appreciation of biologists for the newer researches in insect physiology and behavior.

No volume attempting to provide even a partial survey of biological progress could afford to ignore the phenomenal interpenetration of physiology and biochemistry which is taking place in both plant and animal biology at the present time. On the one hand, the biochemist is becoming aware that cells are not mere bags of enzymes, substrates, and products; on the other, the physiologist is learning that it is intrinsically impossible to explain physiological processes except by way of a fundamental biochemical approach. This interrelationship of fields is well illustrated in the two final contributions to the present volume of the series. Animal hormones cannot be understood simply in terms of where they are produced and on what end-organs they have a specific effect. The action of hormones on cells is ultimately biochemical. This, however, need not mean that hormones always control the rates of specific processes by modifying the reactions of enzymes with their substrates. It is also possible, and in many instances, as Rachmiel Levine points out, even more likely that the control is exerted by modifying the access of substrate to enzyme system. Membrane permeability is coming even more strongly to the fore than in earlier physiology, and already the biochemist is beginning to talk about "permeases," which may or may not be themselves enzymatic.

George G. Laties' survey deals with another aspect of regulation: the control of cellular work, including growth and development, by oxidative phosphorylation; the dependence of oxidative phosphorylation on the respiratory rate; and, most interestingly, the regulation of respiratory rate itself by a sort of feedback mechanism, through the availability of phosphate acceptors in the cell. Thus, by regulating the supply of phosphate acceptors such as adenosine diphosphate, the energy-consuming processes of growth and maturation may to a certain degree adaptively regulate the rate of respiration, analogously to the regulation of the respiratory rate by the piling up of an oxygen debt, and ultimate production of carbon dioxide, through muscle contraction. It would be extremely interesting to examine a similar review relating to animal instead of plant metabolism.

From a mountain top one cannot look in every direction at once. It is enough that this third volume of the SURVEY OF BIOLOGICAL PROGRESS can offer six reviews of such insight and stimulating quality. The succeeding volumes will endeavor to maintain their level of excellence and to fill in the remainder of the biological panorama.

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Embryological Concepts in the Twentieth Century[1]

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I. INTRODUCTION

It was an embryologist who wrote that "Die Madonna della Sedia nimmt sich auf 1 cm Entfernung mit der Lupe betrachtet auch anders aus, als auf 5 m Distanz. Das erste Mal sehen wir nur Klexe," and who then raised the question: "Ist denn das Studium von Klexen wirklich die einzige Aufgabe des Biologen?"[2] (Driesch, 1894, p. 163). An intellectual historian concerned with the history of biology might well ask himself a similar question with respect to the subject or object of his studies, substituting the parameter of time for that of space, and he might justifiably regard as formidable the difficulties of establishing the interrelationships of ideas evolving during the period which includes his own development. If, however, there is any truth in the so frequently repeated truism that the ideas of the present can properly be understood only in the light of their precursors, in the same manner that an event in the development of an embryo can be fully comprehended only in terms of the previous events which have led up to it, there is no period to which it is more desirable for the practising scientist to apply the techniques of intellectual history than the stage immediately preceding his own.

For embryology, at least, there has been no dearth of preliminary attempts to trace sequences of ideas from the time of antiquity towards

[1] An expansion of an address by the same title delivered as part of the Presidential Symposium of the American Society of Zoologists at the meetings of the American Institute of Biological Sciences in East Lansing, Michigan, in September, 1955.

[2] The *Madonna of the Chair* examined with a lens at a distance of 1 cm shows up quite differently than at 5 m away. The first time we see only blotches. Is then the study of blotches really the only task of the biologist?

the 1900's (Bilikiewicz, 1932; Needham, 1934; Meyer, 1939; Oppenheimer, 1955a). The development of specific concepts of morphogenesis within the 20th century has also recently been treated most thoughtfully by Seidel (1955) and by Bautzmann (1955) in lectures presented at a 1954 meeting of the Gesellschaft Deutscher Naturforscher und Ärzte. The task at hand therefore might seem to simplify itself to the further pursuit into the middle of the 20th century of the same concepts that have been followed into the 19th.

While the difficulties of acquiring perspective on contemporary ideas are obvious—in fact, perhaps because they are obvious—they are not insuperable. One need only remember, to pass for a moment into other fields, Einstein and Freud, the impact of whose ideas can at midcentury surely be estimated with considerable accuracy. Now these are extreme examples, to be sure. Embryology has never bred any counterparts of Einstein and Freud, and questions concerning the sphere of influence of ideas originating from particular embryologists can be framed only with reference to lesser luminaries than these. But if the skies of embryology have lacked such suns, they have been decorated by a number of stars of the first magnitude. For the sake of attempting to estimate how their successors a half century later may have reacted to their contributions, let us return for a moment to some of the investigators who shone in embryology towards the beginning and the end of the 19th century.

Pander was almost certainly appreciated 50 years after his prime in quite the same way in which we value him now: witness Kölliker, who wrote in 1861 (pp. 8–9):

> "PANDER'S . . . Untersuchungen . . . geben nicht nur eine genauere Geschichte der allerersten Entwicklung des Hühnchens, als man sie bisher besass, sondern waren vor Allem dadurch von grösster Tragweite, dass durch dieselben zum ersten Male die ursprünglichen, von WOLFF geahnten Primitivorgane, die der Entwicklung der Organe und Systeme zu Grunde liegen, durch die Beobachtung nachgewiesen wurden. PANDER unterscheidet an der Keimhaut des Hühnereies schon in der zwölften Stunde der Bebrütung zwei Schichten, eine äussere . . . und eine innere . . . zwischen welchen dann später noch eine dritte Lage . . . sich entwickelt. Obschon nun PANDER diese Blätter als den Ausgangspunct aller spätern Organe betrachtet, so hat er sich doch über ihre Umwandlungen und ihre Bedeutung im Ganzen genommen nur sehr kurz ausgesprochen und wären wegen des Aphoristischen seiner Darstellung seine Angaben wohl nicht so bald zu

einer grösseren Bedeutung gelangt, wenn dieselben nicht in v. BAER einen Förderer und theilweise auch einen Vertreter gefunden hätten, der es verstand, der Blättertheorie in den weitesten Kreisen Eingang zu verschaffen."[3]

Haeckel, in contrast, fifty years after his moment in history was certainly evaluated quite differently than we interpret him today: Kerr in a brief history of the germ layer theory published in 1919 could write (p. 506) of the *Gastraea* theory quite factually and uncritically that:

> "Haeckel . . . about the same time as Lankester also developed the idea that the diploblastic stage of ontogeny was to be interpreted as the repetition of an ancestral form: Haeckel called this ancestral form *Gastraea.* The main difference between Haeckel's view and Lankester's was that the former regarded the endoderm as having arisen by a process of invagination—as it actually does arise in ontogeny in the great majority of cases—while Lankester regarded it as having arisen by a process of delamination from the outer layer."

He terminated his historical discussion of the establishment of the germ layer theory (published, it may be noticed, the year after Spemann's first exhaustive communication on the relationships of the layers during gastrulation) with only a single and rather insignificant reservation: "The author regards as the chief qualification of the germ layer theory indicated by modern work . . . that the boundary between two layers where they are continued into one another must be regarded not as a sharply marked line but as a more or less broad debatable zone" (Kerr, 1919). It is an interesting and perhaps meaningful fact that the view expressed a half century later concerning the contribution of Pander, who flourished early in the 19th century, has changed less during the ensuing years that the evaluation, after an approximate half century, of Haeckel who worked closer to our own time; clearly the passage of time as

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[3] Pander's investigations not only present a more exact history of the earliest development of the chick than was previously available; but they were of the greatest importance since it was through these studies that the primitive organs, foreseen by Wolff, which lie at the basis of the development of later organs and tissues, were for the first time authenticated by observation. Pander distinguished two layers in the blastoderm of the chick, an outer . . . and an inner . . . between which a third layer . . . later develops. Although Pander considered these layers as the point of origin of all later organs, yet he expressed himself only very briefly concerning their transformations and general significance; and because of the aphoristic manner of his presentation his statements would not so soon have attained their great significance had they not found in von Baer a promoter and partly an advocate who understood how to bring the layer theory into fashion in the widest circles.

measured in years is not the only factor involved in the acquisition of historical perspective.

The choice of Pander and Haeckel for examples has not been haphazard. These investigators are appropriate as illustrations since they can be said, in a qualified simplification, to have represented in a way the beginning and the end of the development of the germ layer theory that dominated the embryology of the 19th century: Pander the beginning, since he first put on a sound observational basis what Wolff had extracted from natural philosophy; Haeckel the end, since he stretched what had been observed by his time into a theoretical framework so taut that whatever tenuous relations might otherwise have been maintained between the germ layer concept and biological reality were severed as a result of its artificial overextension.

If maintaining an attitude of reverence for the germ layers seems to us from our vantage point to represent a prevailing intellectual habit of a majority of 19th century embryologists, what often appears to us to exemplify the equivalent frame of mind at the turn of the century is the outlook which characterized the investigators who followed soon after Haeckel—Roux, Driesch, Herbst, Boveri, O. Hertwig, Spemann, and Harrison; and we often say glibly of these, that they modernized embryology by making it experimental. The implication is thus very frequently drawn that the embryology characteristic of the 19th century was static, as contrasted with the more dynamic developmental physiology of the 20th. There is a strong fallacy in this argument which ignores the very evident facts that Pander and von Baer were just as profoundly concerned with change as we are today, and that those later 19th century investigators who patiently developed the germ layer theory had themselves a broad general background and a consequent wide variety of embryological interests. The customary and frequent opposition of 19th century embryology as morphological to that of the 20th century as experimental is further misleading in that it accentuates the use of the experimental method as an end in itself rather than as an adjunct to the descriptive method which deals with the more obvious embryonic features. It confuses the content of what was studied with the manner of its studying, and quite obscures what may well prove to be a much more incisive distinction between the exertions of this science as carried out before and after the turn of the century.

First to concentrate briefly on method, it might to some persons seem a closer approximation to accuracy to generalize that the methods of the 19th century were descriptive, while those of the 20th are analytical, and that a difference between the 19th century and the 20th may be that the latter has penetrated beyond the horizons of the former through the elaboration of special techniques. This contention may well hold true for many fields of biology, but it is not adequate for the case of embryology.

In the first place, the application of the new experimental method to embryology was initiated considerably earlier in the 19th century than is commonly admitted. It is no secret (Schleip, 1929), though it is not commonly bruited about, that in 1869 Haeckel himself, with whom Roux was to start studying the following year, published the results of experimental division of siphonophore larvae, demonstrating that half-larvae were able to form whole organisms. But if initiation of the experimental method, so often said to be the special contribution of the innovators of the changed embryology, was both possible and actual a third of the way back into the 19th century, this is not the only example where the specific chronology of events distorts our perspective. A further complication is that the methods used by experimental embryologists well into the 20th century in their stark and beautiful simplicity were essentially 19th century methods. Roux killed the frog's blastomere by a cautery needle in fact as brutal as the amputation iron of Paré; and what were the first tools of Spemann but a lens, a dish, and a loop of hair?

If a clear division between the methods of 19th century and 20th century embryology seems blurred by such considerations, it is possible that a sharper line can be drawn between the two periods by considering the nature of the problems investigated during the two periods. It might be held that the 19th century was more single-minded; and viewed retrospectively this may be a greater significance of the 19th century germ layer theory than that it was established by morphological techniques. The investigators in the 19th century, sprung as they were from *Naturphilosophie*, were inspirited with an idea which became the germ layer theory, a concept recognizable as such even to those who have difficulty in defining concepts in biology; and this doctrine, subject as it became through the efforts of Haeckel to the unifying control of the evolutionary concept of Unity of Descent, was a centralized and centralizing concept for the whole century, losing little of its sovereignty in 19th century embryology even after the general acceptance of the cell theory and even though much other embryological work of varied nature was completed.

The investigators at the turn into the 20th century, in contrast, no longer centered their efforts on one focus. It is the essence of 20th century embryology that it has not limited itself, until fairly recently, to concentration on a single specific idea. Its earliest workers were astonishing at the first for their widening curiosity. True, at the backs of their minds lay the problem of progressive differentiation, but here they differed little from their predecessors of the 19th century or of all the centuries since Aristotle. The great difference became that their questions were more eclectic and thus provided a strong revitalizing impulse towards the production of new ideas, for the solution of which they invented transitory not permanent technical approaches. What does a blastomere do in the absence of its sisters? How does an embryo develop when you cut off its tail? What happens when you shake an egg to pieces? or if you cut away some of its protoplasm? or if you whirl it around or turn it upside down? or if you put it into a solution as improbable of developmental significance as lithium? It was a hallmark of the work of the turn of the century that when the new experimental method was turned toward devising a crucial experiment, the question to be answered was one that had been framed earlier by older and other methods (e.g. Harrison's introduction in 1907 of the tissue culture technique to verify a former hypothesis that the neuroblast is the source of the outgrowing axone); otherwise the inquiries were at the start to a considerable degree undirected.

Roux himself, to be sure, might not have concurred with this interpretation, and it is not to be denied that he and others of his time were men of ideas. Great volumes of theoretical discussion poured from his own pen and from that of Driesch, and Roux as well as Driesch eventually abandoned actual experimentation in favor of theorizing. But while the Roux-Weismann theory, for instance, stimulated considerable attention to the possibilities of its experimental confirmation or invalidation, this theory never matched the intellectual dominance attained by the germ layer theory before it, and it remained a proclivity of a majority of the early experimentalists that they were men of many ideas and not just a single one. And even when the contemporaries and immediate followers of Roux and Driesch started their experiments out of theoretical considerations, it is quite possible that they often forgot their ideas in their joy at being able at last to play with the embryo as they would. No one who has ever operated on a living embryo can ever believe but that when the early experimentalists carried out their manipulations they did so in large part because of their sheer pleasure in doing so. Whatever their motivation, it can hardly have worked to the detriment of embryology that they diversified their interests instead of concentrating them, since thereby they opened the many new avenues of investigation whose divergence characterizes the entrance to the modern scene.

The fact remains, however, that the generalization of the early experimental results on a profound theoretical level had to await the passage of approximately a third of the 20th century. Spemann's (1936, 1938)

Silliman Lectures at Yale, which looked somewhat in the direction of the past, and Harrison's (1945) Address at the Harvard Tercentenary, which faced squarely into the future, were not delivered until the 1930's (in 1933 and 1936, respectively; Harrison's Silliman Lectures, delivered in 1949, have not yet appeared in print).[4] Pantin (1955) has recently set 1918 as the date for biology's breaking of tradition with its morphological past. For embryology, the change was a gradual one, from 1869 through to the 1930's, and it may or may not be significant that the midpoint of the transition was passed close to the turn of the century.

It is quite often said, by those who try to outline the methods by which science operates, that a first phase in its development consists of the observation of data, a second, of their classification, and that there finally follows an inquiry into their relationships. If there is any single generalization that can be safely formulated concerning the history of embryology as a whole, it is probably that this science has carried out all these procedures simultaneously at all phases of its development, from the time of Aristotle through to our own.

It can be argued, on the other hand, that embryos were first studied as whole organisms (Aristotle, Fabricius, Harvey, Malpighi, Wolff), then in terms of their constituent layers (Wolff, Pander, von Baer, His, Haeckel, Spemann), next in relationship to their constituent cells (Roux, Driesch, all the students of cell lineage, Spemann, Harrison), and finally with reference to the components of cells, through the 19th century largely nuclear (O. Hertwig, Boveri) though in some cases visible cytoplasmic inclusions were also investigated (Boveri, E. B. Wilson, Conklin). It is hardly necessary to point out that the 20th century continues the process by describing and analyzing both the visible and invisible nuclear and cytoplasmic elements of the cell in terms of their constituent molecules.

The integrative powers of the embryo, at all of its levels, are however so pervasive that they never permit themselves to be overlooked by those who avail themselves of the privilege of looking at the embryo at all. The result has been that when each of the practices just enumerated became fashionable, the previous one was never completely outmoded; and when, at each stage of its development, embryology has added a new dimension to its studies, it has never wholly discarded the old ones. Spe-

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[4] Harrison's Silliman Lectures were entitled "Organization and Development of the Embryo." The titles of the six individual lectures were: Introduction; The Egg and Early Stages of Development; Autonomy and Mutual Dependence of Cells; The Nervous System; The Symmetry of Organisms; and Development and Growth in Complex Systems.