Shifting Assumptions in American Biology: Embryology, 1890-1910

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INTRODUCTION: THE DISTORTION OF DICHOTOMIES

The presumed dichotomy between continuity and discontinuity has played a role at many levels throughout history. Whether the world consists of continuities or discrete units has been a subject of controversy for scientists and philosophers for millennia. Similarly, the question of whether scientific patterns have changed continuously or discontinuously has stimulated discussion among generations of historians and philosophers of science.[1] Most of the latter, though not all, have agreed that science has crystallized at times into relatively coherent efforts that go beyond purely individualized, subjective contributions. These shared pursuits have been variously defined as disciplines (Toulmin), fields (Darden), research programs (Lakatos), or research traditions (Laudan), for example. Some maintain that change in those efforts or in loyalty to one area or another happens gradually and according to an evolutionary pattern (Toulmin), while others emphasize rapid and revolutionary change (Kuhn).[2] Historians of biology in particular have come increasingly to adopt the view that scientific change has been rapid and discontinuous, though not all historians have adopted the

1. See Everett Mendelsohn, "The Continuous and the Discrete in the History of Science," in O. G. Brim, Jr., and J. Kagan, ed., *Constancy and Change in Human Development* (Cambridge, Mass.: Harvard University Press, 1980), pp. 75-112, for discussion of this subject.

2. See Stephen Toulmin, *Human Understanding* (Princeton: Princeton University Press, 1972); Lindley Darden, "Discovery of the Emergence of New Fields in Science," *Phil. Sci. Assoc., 1* (1978), 149-160; Darden, "Theory Construction in Genetics," in T. Nickles, ed., *Scientific Discovery: Case Studies* (Dordrecht, Holland: D. Reidel, 1980), pp. 151-170; Imre Lakatos, "Falsification and the Methodology of Scientific Research Programmes," in Lakatos and Alan Musgrave, ed., *Criticism and the Growth of Knowledge* (Cambridge: Cambridge University Press, 1970); Lakatos, "Proofs and Refutations," *Brit. J. Phil. Sci., 14* (1963), 1-25, 120-139, 221-243, 296-342; Larry Laudan, *Progress and Its Problems* (Berkeley: University of California Press, 1977); Thomas Kuhn, *The Structure of Scientific Revolutions* (Chicago: University of Chicago Press, 1962).

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Kuhnian idea of revolution, in which the result must be incommensurable in some significant way with the original; they simply mean that individuals or groups rejected older ideas and hence speeded change.[3]

The period 1890-1910 has often been chosen as a case study in the history of modern American biology, for it seems to prominent historians of modern biology such as Garland Allen that biology underwent major revision in that period. As Allen sees it, there was a revolt in biology, away from speculative, descriptive natural history toward modern, analytical, and experimental science.[4] In his view, the naturalist gave way to the experimental biologist – a view that I find misleading because the meaning of these terms changed in fundamental ways during the period in question.

Setting aside for the moment the historical question of what actually occurred in turn-of-the-century biology, I maintain that endorsing such a revolutionary view of how science changes risks distorting the facts in the effort to illustrate the expected patterns. Since one era's radical often becomes the next generation's conservative, focusing on dichotomies and disputes causes problems as the historian moves from one era to another and the terms and disagreements change. Perhaps a revolutionary model will appear most appropriate in some cases. An evolutionary pattern may seem to hold in other cases.

Rather than imposing either of these two models on history by actively looking for patterns of discontinuity or continuity, it will maximize the chances of achieving historical accuracy to begin by delineating a range of possible interpretations of scientific history – perhaps a range more full than is actually exemplified in the literature. Since I seek to achieve historical accuracy in this paper, I shall sketch briefly some continua of scientific assumptions that I have found useful for this discussion. The list is not intened to be perfect or exclusive; rather, it represents working suggestions that I have found helpful in dealing with the available data in a way not characteristic either of the revolutionary models of the history of science, in which one may have to force the data to identify discrete areas undergoing change, or of the evolutionary models, in which the real changes may be overlooked in emphasizing the continuities. After suggesting these continua I shall proceed to examine the work of four individuals generally agreed to be central to the emergence of modern American experimental biology – Edmund Beecher Wilson, Edwin Grant Conklin, Thomas Hunt Morgan, and Ross Granville Harrison.[5] I shall then illustrate how my use of continua has led me to conclusions that capture essential elements of turn-of-the-century biology that have been generally overlooked because of the predominance of historiographic approaches stressing discontinuities.

The basic useful continua of possible assumptions (not to be confused with a continuous historical view) represent what methods and approaches scientists adopt, what terms they use, what problems they address, and what types of results they seek. The first, a methodological continuum, ranges from the most passive observation at one extreme, through systematic observation and description, comparative description, and use of manipulative experimental techniques or methods, to a fully experimental approach at the other extreme. Passive observation involves simply looking at what occurs without human interference, while experimentation involves manipulating organisms in order to obtain additional data, which are then also observed and described. Experimentation thus incorporates both descriptive and comparative methods. We therefore have here not a distinction between observation and experimental methods, but a range of degrees to which and ways in which observation and experimental manipulations can be employed. It may turn out that at times, historically, there have been opposing camps of experimentalists and observers, for example, but let us not impose these dichotomies where they are not appropriate.

This continuum gains importance here because of the particular changing assumptions of the 1880s and 1890s. The numerous researchers carrying out cell-lineage studies at Woods Hole, Massachusetts, in that period, whom Allen cites as early experimenters, used only the simplest of experimental techniques for preparing specimens in their investigation of the development lineage of individual cells during the

3. See Garland Allen, *Life Science in the Twentieth Century* (Cambridge: Cambridge University Press, 1978); Donna Haraway, *Crystals, Fabrics, and Fields* (New Haven: Yale University Press, 1976).

4. Allen, especially *Life Science*; Allen, "Naturalists and Experimentalists: The Genotype and the Phenotype," *Stud. Hist. Biol., 3* (1979), 179-209; Allen, "The Transformation of a Science: Thomas Hunt Morgan and the Emergence of a New American Biology," in Alexandra Oleson and John Voss, ed., *Organization of Knowledge in Modern America, 1860-1920* (Baltimore: Johns Hopkins University Press, 1979), pp. 123-210.

5. See Allen, *Life Science*, p. 35; *What is Life?* Johns Hopkins University Fiftieth Anniversary pamphlet (Baltimore, 1925), p. 18: "If anyone conversant with the field of zoology were asked to choose six outstanding American leaders in this science, four Johns Hopkins alumni, in most instances would be included – Morgan, Wilson, Conklin, Harrison." The pamphlet does not say who the other two would be.

earliest stages of embryonic development.[6] These cell-lineage researchers basically asked descriptive questions and employed nondisruptive methodologies to study normal development. Some of these men, joined by others investigators such as Morgan and Jacques Loeb, then went a step further, asking such questions as what will happen if the egg is shaken, cut, or exposed to other abnormal chemical or physical conditions. These, too, are essentially descriptive (what if . . . ?) questions that can be answered by using basic manipulative experimental techniques. This research therefore lies at a slightly different place on the continuum than the earlier cell-lineage research, but certainly the change in methodology was not revolutionary.

Beyond these simple experimental techniques, there are increasingly complex experimental techniques. And at the extreme there is what I call an experimental approach, which utilizes experimental manipulations and techniques but also involves a more general research methodology, with different implications about what types of questions are appropriate. The experimental approach demands that the researchers control their material even further by formulating a hypothesis concerning a specific, narrowly focused question, and then determining whether the data support that hypothesis or not. This approach entails the auxiliary hypothesis that actively manipulating biological material and producing abnormal specimens can reveal information about normal conditions. A fully experimental approach seems to produce identifiable and immediate results, as long as the experiments are successfully designed.

Ontologically, biology covers a continuum ranging from mechanistic materialism to vitalism. Though not central to my discussion of experimental embryology here, ontological assumptions were important generally in turn-of-the century biology. As Charles Otis Whitman urged in 1894, in an essay addressed to the Marine Biological Laboratory at Woods Hole, the tendency to dichotomize into mechanism versus vitalism is destructive and confuses the important questions.[7] This does not, of course, mean that all possible positions have been represented, or deny that real antagonisms have existed at various times historically. Rather, I am urging that the tendency to classify and to dichotomize may distort the facts.

6. See Jane Maienschein, "Cell Lineage, Ancestral Reminiscence, and the Biogenetic Law," *J. Hist. Biol.*, *11* (1978), 129-158, for discussion of cell-lineage work. Also, Jeffrey Werdinger's Ph.D. diss., Indiana University, 1980, on the Marine Biological Laboratory discusses this work in some detail.

7. Charles Otis Whitman, "Prefatory Note," *Biol. Lect.*, 1894 (1895), iii-vii.

The type of problems addressed and type of results sought also exhibit a range, and it is perhaps here that we can see the most significant, or self-conscious, differences in embryology in the period in question. Possible problems range from the most general concern with "what is life" or "what causes development," for example, to such extremely narrowly focused questions as what a part of a chromosome does at a particular stage.

Types of results sought similarly range from descriptions, to yes or no answers, to particular narrowly defined questions such as "will this organism do such and such under certain specified conditions," to broad "umbrella" theories capable of explaining a wide range of dissimilar phenomena, such as Darwin's theory of evolution by natural selection.

These ranges of methods, ontological commitments, problems, and results are not always neatly separable, of course. Sometimes an overriding concern with particular methods or problems, for example, will dictate the ontology or type of results. Thus a full understanding of scientific change must take into account connections among these commitments as well as the particular commitments themselves, but tracing the complicated connections is a task for another study.

Returning to the period 1890-1910 in American biology, I, like the generation of American biologists in question, see not one primary dichotomy in biological science but a range of issues, with a multitude of different but compatible sides. There was no general overriding concern with experimental methods *in contrast to* description, or functional questions *as opposed to* evolutionary considerations, as Allen maintains. Rather, the leading American biologists of the period sought to reorder and redefine a variety of assumptions about appropriate research problems, methodological assumptions, and other, auxiliary hypotheses.

Turn-of-the-century biology holds special significance precisely because a number of Americans sought to establish a unified science of biology that would break down the old antagonisms: between field and laboratory workers, between zoologists and medical researchers, between evolutionists and physiologists, for example. They did not deny that different individuals ought to do different research, of course, but they sought to redefine what they considered appropriate assumptions about problems and methods. By self-consciously and actively considering the proper domain and appropriate methods for research, each individual generated what he considered a productive research program for confronting his chosen problems, often newly defined or approached with a new emphasis.[8] Though he formed his own, he did not reject other programs.

E. B. Wilson, in an often quoted article of 1901, sought to demonstrate that biology had moved beyond its previous antagonistic divisions into naturalist and physiologist factions. "We may well congratulate ourselves, on such a solidification of aim and on the accompanying increase in the exactness and order of our method [partly] . . . through the revival of interest in natural history, in the older sense of the word, that has accompanied it," Wilson wrote. "With these changes has come a better understanding between the field naturalist and the laboratory morphologist and physiologist, who in earlier days did not always live on the best of terms." Arrogance by the experimentalists is undesirable, Wilson urged, because the comparative method is also very important. Although the experimental method may seem to yield the greatest results for the immediate future, "let us not depreciate the importance of the comparative study of normal phenomena to which biology already owes so many brilliant triumphs."[9]

This theme recurs repeatedly in the writings of all the American protagonists of the period. It is *not* appropriate to conclude, with Allen, that such passages serve mainly to illustrate that a naturalist-experimentalist dichotomy existed.[10] Rather, the reiterated concern with appreciating both observation and experiment, both naturalist/field and laboratory research, and both evolutionary and physiological questions shows that such a disagreement probably had existed earlier but that these Americans differed in part from their predecessors precisely because they wished to move beyond such disputes.

8. "Research program" is not meant necessarily in Lakatos's sense, but as a commonsense term referring to a set of problems, methods, and goals. Elements of Toulmin's disciplines, Darden's fields, Lakatos's programs, and Laudan's traditions are compatible.

9. Edmund Beecher Wilson, "Aims and Methods of Study in Natural History," *Science, 13* (1901), 18, 19, 22.

10. Allen, in "Naturalists and Experimentalists," pp. 181-186, esp. p. 183, refers to Whitman's and Wilson's lamentation on the "uselessness of the dichotomy between descriptive and experimental work," but he continues nonetheless to stress the dichotomy in the period and for the individuals in question. In "Transformation," p. 177, he concludes that "the tension between the naturalist and the experimentalist in American science is perhaps nowhere better illustrated than in the career of Thomas Hunt Morgan." This insistence that dichotomies had existed, that some sought to defuse them, but that they still were basic seems problematic. It is the dissolution of the old dichotomies by the Americans, including Morgan, that I seek to clarify.

My task in this paper is to show the ways in which the particular study of individual development changed because of the self-conscious reworking of assumptions about what biology should be like. Experimental embryology appeared as a defined research area after the German work of the 1870s and 1880s, and embryological experiments were undertaken by many of the Americans. This paper therefore briefly outlines the emergence of the experimental embryological program in the 1880s. It then discusses each of the principal American figures, illustrating what actually occurred in each individual's work in order to demonstrate the way in which the science changed as the basic assumptions about what science should be like changed.

EXPERIMENTAL EMBRYOLOGY

As has been discussed elsewhere in more detail, for Ernst Haeckel the phylogenetic past of an organism causally determines and therefore explains the ontogenetic stages through which the individual passes.[11] No further explanation is needed, for Haeckel; differentiation occurs because it is determined by the appropriate phylogeny. Haeckel's work served to emphasize study of the embryo, albeit as an evolutionary product above all, but it shut off further investigation into the reasons for emerging differentiation, which the next generation of biological researchers came to see as the most interesting problem of development.

The publication by Wilhelm His in 1874 of *Unsere Körperform* called Haeckel's program into question, but even further stressed the value of embryological studies.[12] For His, parts of the embryo are not preformed in the germ, nor is differentiation preexistent. But the causes of differentiated form already exist in the materials of the egg, which are prelocalized and arranged approximately as they will be in the embryo and in the adult form. Thus, His essentially projected later organization onto the egg. In his view, the differentiated form of the parts occurs because of unequal growth of an unhomogeneous egg cell, which has its "organ-forming germ regions." His's polemical discourse provided a principle for development, but not a fully articulated theory accounting for the causes of, or explaning, embryonic development, specifically

11. See Jane Oppenheimer, *Essays in the History of Embryology and Biology* (Cambridge, Mass.: MIT Press, 1967), Edward Stuart Russell, *Form and Function* (London: John Murray, 1916), esp. chap. 14, pp. 246-260.

12. Wilhelm His, *Unsere Körperform u. das physiologische Problem ihrer Entstehung: Briefe an einen befreundeten Naturforscher* (Leipzig: FCW Vogel, 1874).

differentiation. Yet because his work suggested that early stages should reveal preorganization, it stimulated various theories to determine exactly how early and where in the embryo differentiation occurs.

Within a few years of His's work, others offered alternative views and theories to explain how the egg becomes differentiated into an adult – *the* problem of development that Haeckel had left unanswered. Eduard Pflüger, for example, stressed the crucial role of external conditions for directing differentiation of the essentially homogeneous egg. Gustav Born endorsed the opposite view that redistribution of egg segments and cleavage stages plays a basic part, so that internal redirection within the initially homogeneous egg determines differentiation. Wilhelm Roux maintained that many aspects of development are self-differentiating, resulting from unequal growth of different materials within the egg; these he called independent differentiation. At the same time, other differentiation processes rely on interactions with other cells and other body parts; these he labeled dependent differentiation. The whole developmental process begins with a qualitatively unequal, hence by definition differentiated, division of the cytoplasm *and* nuclear material, which produces a mosaic of different cells. In contrast, Hans Driesch and Oscar Hertwig asserted that the various blastomeres are not differentiated at early stages of development, that differentiation occurs later, gradually (epigenetically), as cell division and cellular interaction progress.[13]

These theories capture the range of possibilities: the egg is actually differentiated from the beginning, so that the key to understanding developmental processes lies in heredity; or the egg is undifferentiated

13. These men's ideas were expressed in various papers; the following are relatively accessible: Eduard Pflüger, "Über den Einfluss der Schwerkraft auf die Theilung der Zellen," *Archiv für die gesammte Physiologie des Menschen u. der Thiere, 31 (1883), 311-318*; Gustav Born "Über Verwachsungsversuche mit Amphibienlarven," *Archiv für Enwickelungsmechanik der Organismen, 4* (1896), 349-465, 517-623; Wilhelm Roux, "Contributions to the Developmental Mechanics of the Embryo . . . ," in Benjamin Willier and Jane Oppenheimer, ed., *Foundations of Experimental Embryology* (Englewood Cliffs, N.J.: Prentice-Hall, 1964), pp. 2-37; Roux "The Problems, Methods, and Scope of Developmental Mechanics," trans. William Morton Wheeler, *Biol. Lect.*, 1894 (1895), 149-190; Hans Driesch, *Analytische Theorie der organischen Entwicklung* (Leipzig: Wilhelm Engelmann, 1894); Oscar Hertwig, "Welchen Einfluss ubt die Schwerkraft auf die Theilung der Zellen," *Jenaische Zeitung Naturwissenschaft, 18* (1884-1885), 175-205; or Hertwig, *Zeit- u. Streitfragen der Biologie* (Jena: Gustav Fischer, 1894); Frederick Churchill, "Wihelm Roux and a Program for Embryology," Ph.D. diss., Harvard University, 1966.

completely, and interaction of cells or environmental and other external conditions determine all. Even such highly publicized attempts as Roux's, Driesch's, and Morgan's studies of half embryos proved inconclusive in deciding when and how differentiation occurs.[14]

In the 1890s the various observations and hypotheses continued to excite considerable discussion and stimulate the seach for new, conclusive data. What was new in this generation of German-developed theories was the union of a changing emphasis and changing basic problems in embryology with an emerging endorsement of a more fully articulated research methodology. This emerging experimental methodology seemed to the generation of followers an appropriate way of accomplishing their shared primary aim of assessing the facts of differentiation and explaining questions about developing differentiation in causal, analytical, materialistic terms.[15] For embryology, instead of studying the embryo mainly to reveal phylogenetic relationships by uncovering anatomical similarities, the new group of embryologists sought to understand the internal causal mechanisms by which the embryo develops on its own.

It is essential – and historians have erred on this point – to emphasize that these embryologists and the generation of Americans that followed were not forsaking the earlier concern with evolutionary and morphological or even "naturalist" questions; on the contrary, they thought they saw a new way to explore both evolutionary and anatomical concerns by studying the embryo with a new emphasis. As E. B. Wilson stressed throughout the first edition of his *The Cell in Development and Inheritance*, both the nucleus, which seemed to him to provide the material of inheritance, and the cytoplasm are essential to the development of an individual, which is, as a whole, a product of evolution.[16] In 1899, T.H. Morgan expressed the new interests perfectly in a critique of Weismann's general theories. "The problems that they are trying to solve are those that Weismann also tries to answer," Morgan wrote,

but "the younger investigators" base their interpretations on the

14. Roux, "Contributions"; Driesch, "The Potency of the First Two Cleavage Cells in Echinoderm Development . . . ," in Willier and Oppenheimer, ed., *Foundations*, pp. 38-50; for Morgan, see below.

15. To judge from citations, Driesch served as exemplar for this materialist program. The Americans seemed much more sympathetic to Driesch and relatively critical of Roux.

16. Wilson, *The Cell in Development and Inheritance* (New York, 1896; reprint. ed., New York: Johson Reprint Corporation, 1966).

assumption that when a change takes place a sufficient cause for the change is to be sought in the organ itself and in the external conditions surrounding that organ. They are not content to rest their "explanations" on "the phyletic origins" of the changes. It is not necessary to deny the theory of descent, but it is unsafe and in many cases unscientific to base "causal explanations" on an imaginary line of ancestors.[17]

For the experimental embryologists, then, the embryo was essentially a mini-organism uniting both evolutionary and individual embryological elements. The various investigators were endorsing many of the old concerns, but in stressing the need to achieve answers to analytical causal questions about differentiation and to obtain results, they advocated different emphases and different methods.

THE AMERICANS

The Americans central to the emergence of "modern" American embryology include the Johns Hopkins gang of four – Wilson, Conklin, Morgan, Harrison – who all studied under the only morphologist in the Johns Hopkins graduate school, William Keith Brooks.[18] Although others played important roles in American biology, these four were by 1910 regarded as outstanding leaders in American biology.[19] In particular, these four each worked through the various assumptions and theories about development, and each came by 1910 to articulate his own specialized research program growing out of shared earlier concerns. I will therefore sketch briefly, in turn, the evolution of the work of each of these men. Although they later provided overviews and generalizations about their interests that stress different considerations, I have relied for this study only on their work before 1910.[20] This investigation reveals a gradual shift in both problems and methodologies, as each continued to reassess what his scientific inquiry ought to be like in the light of new evidence and new interests.

E. B. Wilson (1856-1939), the oldest, received his Ph.B. degree from Yale's Sheffield Scientific School in 1878. There he studied with Addison Verrill and Sidney Smith, and acquired an enduring interest in traditional natural history. After one year of graduate school at Yale, he moved to Johns Hopkins at the recommendation of a close friend. From Johns Hopkins, he received a Ph.D. in 1881. During 1882-1883, he traveled to Cambridge, England, to work with Michael Foster, to Leipzig to study with Rudolf Leuckart, and to Naples. In Europe he experienced a change of perspective on biological problems, he reported later. After teaching at Williams College, the Massachusetts Institute of Technology, and Bryn Mawr, in 1891 he settled at Columbia.[21]

Wilson's work began with very traditional descriptive studies in 1878. In 1881 for the first time he articulated a concern with "explanation of the steps by which the adult structure . . . may have been acquired," though he did not say what kind of explanation he sought. He expressed interest in "understanding of the causes which have led to certain remarkable methods of development in a number of animal groups."[22] Yet his work remains strictly descriptive and comparative, and no causes are advanced. Another descriptive paper of 1883 reflects a similar concern and suggests that at certain stages form seems "pretty well established."[23]

In 1890, Wilson summarized the goal of morphological studies after Darwin; no longer was the question to be answered simply

what is? it was also *how came it to be*? And this second question, be

17. Thomas Hunt Morgan, "Regeneration: Old and New Interpretations," *Biol. Lect.*, 1899 (1900), 194.

18. See Keith R. Benson, "Problems of Individual Development: Descriptive Embryological Morphology in America," *J. Hist. Biol., 14* (1981), 115-128; William McCullough, "W. K. Brooks's Role in the History of American Biology," *J. Hist. Biol., 2* (1969), 411-438.

19. The other influential biologists include Frank Rattray Lillie and Charles Manning Child at Chicago, Henry van Peters Wilson at North Carolina, Ethan Allen Andrews at Johns Hopkins, and Jacques Loeb, who was not strictly an embryologist.

20. I have read many of the textbooks and archival notes from this period, but for this discussion I have used primarily published articles, since these would seem to reveal best the evolution of basic assumptions about what science should be, which is what I am discussing here.

21. For biographies of Wilson, see H. J. Muller, in *Amer. Nat., 77* (1943), 5-37, 142-172; T. H. Morgan, in *Biog. Mem. Nat. Acad. Sci., 21* (1940), 315-342; Alice Levine Baxter, "Edmund Beecher Wilson and the Problem of Development: From the Germ Layer Theory to the Chromosome Theory of Inheritance," Ph.D. diss., Yale University, 1974, and "Edmund B. Wilson as a Preformationist: Some Reasons for His Acceptance of the Chromosome Theory," *J. Hist., Biol., 9* (1976), 29-57.

22. E. B. Wilson, "The Origin and Significance of the Metamorphosis of Actinotrocha," *Quart. J. Microscopical Sci., 21* (1881), 3-19.

23. E. B. Wilson, "The Development of Renilla," *Philo. Trans. Roy. Soc., 174* (1883), 743.

it observed, is not properly a speculative matter at all, but an historical one; it relates not to an ideal or hypothetical mode of origin, but to a real process that has actually taken place in the past and is to be determined like any other historical event.[24]

To investigate this real process, he decided, he had to question previous emphasis on the germ layers and carefully determine what occurs in the earliest egg stages; hence his endorsement of early cell-lineage studies.

For years the "germ-layer theory" had dominated embryology, Wilson wrote in 1892 after his inspiring visit to Europe, and the result was that "a surprising divergence of opinion exists among the best authorities in regard to some of the most fundamental propositions of this theory." "In what direction may we seek to break away from this deadlock of opinion?" he asked, and concluded that "the only course open to embryological investigation is to examine more precisely the origin of the gastrula itself; *to take as a starting-point not the two-layered gastrula, but the ovum.*"[25] The resulting cell-lineage studies, Wilson concluded, revealed that development is a mosaic of sorts in that each body part begins from a single "protoblast" or group of them. Further analysis of cell lineage reinforced his interpretation that differentiation occurs at an early stage, but he continued to explore exactly at what point and how differentiation is fixed, or determined.

In 1896 and again in 1901, Wilson explained that his experiments on sea urchins supported a non mosaic interpretation of differentiation, like Driesch's or Hertwig's, and showed "how extensively the early stages of development may be modified without affecting the end result."[26] By 1903, he had compared conclusions about numerous organisms produced by various investigators and had found that almost everyone "has reached the conclusion that the immediate factors by which the form of cleavage and the processes of localization and differentiation are determined must be sought in the cytoplasmic organization of the egg."[27] Trying to reconcile that view with his own emphasis

24. E. B. Wilson, "Some Problems of Annelid Morphology," *Biol. Lect.*, 1890 (1891), 53.

25. E. B. Wilson, "The Cell-lineage of Nereis," *J. Morph.*, *6* (1892), 367.

26. E. B. Wilson, *The Cell*, chap. 9, and "Experimental Studies of Cytology, I," *Archiv für Entwickelungsmechanik der Organismen, 12* (1901), 529-596; parts II and III, *13*, pp. 353-395; quotation on p. 377.

27. E. B. Wilson, "Experiments on Cleavage and Localization in the Nemertine-Egg," *Archiv für Entwickelungsmechanik der Organismen, 16* (1903), 438.

on the nucleus as well as the cytoplasm, Wilson cited Theodore Boveri's work and his own evidence that the cytoplasm becomes differentiated or "localized" only after the maturation process has occurred or cleavage has begun. Somehow differentiation begins with a nonvisible base before cleavage; yet cleavage serves to separate the cytoplasmic materials in individual cells, thus determining, or fixing, the differentiation that has already invisibly begun. "The cleavage-mosaic thus becomes in truth a mosaic of specifically different materials and at the same time a mosaic of more or less definitely established tendencies," Wilson concluded.[28]

All of this work of Wilson's, which led him after 1905 further into details of nuclear development, was oriented toward the embryological problem of understanding the precise pattern and the material causes, within the organism itself, of differentiation and determination. Careful observation of cell lineage and of other nuclear and developmental stages provided basic information about what seemed to happen. Comparative studies offered possibilities for general conclusions. And experiments, generally based on manipulating organisms, provided new data, though Wilson did not endorse a fully experimental approach. This period was, for Wilson, devoted to ascertaining the facts about the relatively specific but difficult questions of when the organism becomes differentiated and of using those facts to consider theories and offer tentative suggestions. His evolving refinement of his problems and the type of results he sought directed his intellectual movement along the various continua. Wilson's work exhibits awareness of shifting assumptions and an emerging research program but not a revolt against morphology or rejection of naturalist concerns, which Allen considers central to this period.

Seven years younger than Wilson, Edwin Grant Conklin (1863-1952) obtained his B.A. degree from Ohio Wesleyan and his Ph.D. in 1891 from Johns Hopkins. He taught at Rust University, Ohio Wesleyan, Northwestern, the University of Pennsylvania (1896-1908), and Princeton (1908-1933). Unlike his fellow Johns Hopkins graduates, he did not go to Europe to continue his studies and did not, therefore, receive direct stimulation from the Naples Zoological Station. Yet he participated actively in the establishment of the Marine Biological Laboratory at Woods Hole and remained committed to the research ideal embodied there.[29]

28. Ibid., pp. 448-449, 453.

29. For a biography of Conklin, see E. Newton Harvey in *Biog. Mem. Nat. Acad. Sci.*, *31* (1958), 54-91.

Conklin's early studies are descriptions of structure and development in several organisms. As was typical of work done by Brooks's students, it seems, Conklin's papers reflect a wide reading of the available literatrue on the topics he considered; thus in 1893 he sketched competing ideas and concluded that the nucleus is not the sole bearer of heredity. Rather, he argued, cytoplasmic activity sets such factors as the direction of cleavage and cell size and shape. Some "hereditary tendencies must be transmitted through the cytoplasm," but, echoing Charles Otis Whitman, Conklin concluded that "the *entire* cell is still the ultimate independent unit of organic structure and function."[30]

Studying the cell thus became primary for Conklin, and he urged that careful study is more important than producing overarching theories. "Speculation is valuable only as it is verified by observation and experiment," Conklin wrote in 1896 in reaction to the profusion of opinions coming out of Germany, ". . . and it may be doubted whether it is more profitable for one to continue to start more speculations than a whole generation can run down rather than to take part in hunting down and verifying or rejecting his own speculations."[31] His first contribution to this hunting-down process was a careful, detailed study of cell lineage and embryonic development in *Crepidula*, undertaken for many of the reasons Wilson had turned to cell-lineage studies. "In order to know the significance of cleavage," Conklin urged ". . . it is necessary to know every step in the normal formation of the embryo."[32]

In a general summary paper of 1898, Conklin continued to stress the primary importance of careful descriptive studies, though he was not adverse to using experimental manipulations as well if they proved practicable and helpful in obtaining additional data. All methods must play a role, he wrote:

> Observation, however, is still a valuable method in biology, and it has by no means revealed all that it can, either as to the course or the causes of development. It seems to be assumed in certain quarters that we already know all the important phenomena of normal development and that mere observation is, therefore, a useless and antiquated method. If the time ever comes when every step in the normal development of a single individual is known, the causes of development will not be far to seek. There is no such sharp distinction between observation and experiment in biology as is sometimes assumed; neither method can arrogate to itself a monopoly of certitude regarding facts or causes. In the solution of the problems of development both observation and experiment are necessary; each has its advantages and its disadvantages and one is no less important than the other.[33]

30. Edwin Grant Conklin, "The Fertilization of the Ovum," *Biol. Lect.*, 1893 (1894), 34; On p. 31 Conklin says, "The *independent* unit of structure is still the entire cell, not cytoplasm alone, nor nucleus, but the two together."

31. Conklin, "Weismann on Germinal Selection," *Science, 3* (1896), 857.

32. E. G. Conklin, "The Embryology of Crepidula," *J. Morph., 13* (1897), 5.

Conklin tried to account for the contradictory results that investigators had been finding through their comparative studies. Some cleavage is determinant with respect to later differentiation and other cleavage is not, he explained in a distinction that his contemporaries cited as very useful. He concluded that differentiation usually occurs primarily at earlier stages, even though it seems more prominent at later stages because the changes of cell aggregates are more visible then. Thus the early stages of development remain most critical for investigating differentiation.

And, as Conklin said in 1898 in a lecture at the Marine Biological Laboratory, "The fundamental problems of development and inheritance are in the last analysis questions of differentiation . . . the phenomena of differentiation are therefore of the greatest interest, and their causes one of the most important problems of biology."[34] Maintaining this view, Conklin continued to study early stages of nuclear and cellular differentiation. Relying sometimes solely on description of observation, sometimes on comparative studies, and occasionally on experimental manipulations to produce new data or later to provide information required to test one speculative suggestion or another, Conklin retained his basic interest in differentiation and embryology. In these early years, therefore, his research concerns paralleled Wilson's. Beginning with an understanding of the literature, perhaps as a result of Brooks's teaching methods, Conklin – like Wilson – became aware of the proliferation of theoretical speculations, and during the period 1890-1905 came to understand ever more clearly the need for detailed, reliable data. As he and Wilson succeeded in producing simultaneous cell-lineage studies and comparative analyses beginning in 1892,

33. E. G. Conklin, "Cleavage and Differentiation," *Biol. Lect.*, 1897 (1898), 17-18.

34. E. G. Conklin, "Protoplasmic Movement as a Factor of Differentiation," *Biol. Lect.*, 1898 (1899), 69.

Conklin's views on the causes of development and how to explain them continued to emphasize, in increasingly more subtle ways, cytoplasmic localization and the use of experimental techniques to obtain data. Although they had shared research interests in the 1890s, Wilson later took up studies of the nucleus while Conklin remained committed to the cytoplasm for research. Their research programs diverged, each growing out of independently evolving motion along the continua of assumptions about which problems were interesting and the way to approach them.

T. H. Morgan (1866-1945) is a favorite exemplar of the Americans' endorsement of experimental biology, partly because of his later demonstrable successes in genetics and partly, I suspect, because he became such an articulate spokesman for "modern" experimental biology that some have thought he rejected older methods in biology.[35] It is therefore especially instructive to explore his early work. How did he move along the continua of assumptions about what makes good science?

Morgan completed his B.A. degree in 1886 at the University of Kentucky (then the State College of Kentucky) and his Ph.D. in 1890 at Johns Hopkins. His earliest research included assorted descriptive tidbits on various organisms, leading to his first major work, his dissertation, which appeared in 1891. Tracing the earliest developmental stages to determine to what phylogenetic group the pycnogonids belong, Morgan described in careful detail what happens during early cell cleavage and hoped "to have added a little to our knowledge of the internal changes taking place during development."[36] He used only the simplest of manipulative techniques for fixing specimens. Another paper published in the same year was similar. "The growth and metamorphosis of Tornaria have been thoroughly studied by the modern methods of technique," Morgan wrote.[37] Descriptive in approach, the work incorporated the "modern methods" of specimen preparation. Morgan considered results of comparative studies and suggested ancestral connections, but he did not consider further theoretical issues concerning the causes of development. Other items of embryological

35. For biographies of Morgan, see A. H. Sturtevant in *Biog. Mem. Nat. Acad. Sci., 33* (1959), 283-325; Garland Allen, *Thomas Hunt Morgan* (Princeton: Princeton University Press, 1978).

36. Thomas Hunt Morgan, "A Contribution to the Embryology and Phylogeny of the Pycnogonids," *Stud. Biol. Lab., Johns Hopkins University, 5* (1891), 1–76.

37. T. H. Morgan, "Growth and Metamorphosis of Tornaria," *J. Morph., 5* (1891), 407.

observation, drawn from studies in Jamaica with the Chesapeake Bay program and at the Marine Biological Laboratory, followed. Then in 1893 he published "Experimental Studies on the Teleost Eggs." Designed to use experimental manipulations (which Morgan identified with Pflüger, Roux, Chabry, and Driesch) on fish and to "test" the theory of concrescence in the embryo, Morgan's studies led him to speculations, then to the admission that "perhaps I have stated my conclusion too positively. Any one working at such problems will realize and appreciate the difficulty of correct interpretation of such evasive and complicated phenomena. I should wish therefore to offer the explanation attempted above as an alternative view that may help as a working hypothesis and give stimulus to further inquiry along those lines."[38] He did not, therefore, offer a "test" of his theory in our contemporary sense of the word.

Here Morgan reveals his changing understanding of what science ought to be like. Unlike Conklin, for whom additional speculation was undesirable, for Morgan it was appropriate to offer working hypotheses once one had examined the data and had addressed alternative explanations of the question under consideration about development. His subsequent "Experimental Studies" on echinoderms, frogs, balanoglossus, and fish, undertaken in 1894-1895, reflect similar concerns. In all cases he used simple experimental manipulations, such as sticking an egg to see what would happen, in order to gather data. He then "tested" the various available theories by seeing whether they seemed to accord with the data he gathered with his what-will-happen-if-I-do-such-and-such techniques. Morgan had moved toward using experimental manipulations, but he had hardly endorsed a fully experimental approach as *opposed to* or as a *revolt against* older methods, as Allen implies.[39]

During 1894-1895 Morgan traveled to Europe and, particularly important, he went to the Naples Zoological Station. He cited that event as a turning point, and it is evident that the character of his work began to change afterward. For example, he jumped into the ongoing debate about what happens when two frog blastulae are separated and what the results imply about development.[40] In his

38. T. H. Morgan, "Experimental Studies on the Teleost Eggs," *Anatomischer Anzeiger, 8* (1893), 814. See Edward Manier, "The Experimental Method in Biology: T. H. Morgan and the Theory of the Gene," *Synthese, 20* (1969), 185-205.

39. Allen, *Thomas Hunt Morgan*, chap. 3: "*Entwickelungsmechanik* and the Revolt from Morphology."

40. T. H. Morgan, "The Formation of One Embryo from Two Blastulae,"

publications of 1895, for the first time, Morgan seems to have become concerned with answering relatively specific questions – both descriptive and theoretical. For the first time he also considered the various general theories about differentiation and the way in which adult differentiation becomes established in the early embryo – which Wilson and Conklin had also been investigating. He concluded that "it does not seem that upon any stage of the ontogeny can we throw back all the later stages"; thus His's organ-forming germ regions and Roux's qualitative differentiation both seemed inadequate and misdirected. But Driesch and Hertwig could not be right either in saying that the egg is essentially undifferentiated, for that view was too simple. Some "organic continuity must also be present or established as shown by the experiments which Wilson has made on the eggs of Amphioxus," Morgan concluded, though he did not elaborate further as to what he meant.[41]

Thus Morgan arrived at the same awareness as Wilson and Conklin had reached a few years earlier of how confused the data were and of how inadequate the proposed explanations were for accounting for the causes of differentiation. He moved in a different direction than did Wilson and Conklin, however, and began to study regeneration and heteroplastic grafting as a way of getting information on normal development.[42] He found with heteroplastic grafting experiments of two species that each type of cell retained its particular specific characteristics. Thus cells seemed to be differentiated in those specific characteristics at very early developmental stages. After much study, he suggested a theory about "differences in the chemical substance of the cell itself" during one type of regeneration that he viewed as parallel to normal development. But again he offered his views as a working hypothesis rather than as definitive, since he "hope[d] to have made it clear that the process of regeneration involves many factors."[43]

At first Morgan had been interested in differentiation and determination, a morphological concern that continued with his interest in

Archiv für Entwickelungsmechanik der Organismen, 2 (1895), 65-71; and Morgan, "Half-Embryos and Whole-Embryos from one of the First Two Blastomeres of the Frog's Eggs," *Anatomischer Anzeiger, 10* (1895), 623-628.

41. T. H. Morgan, "Studies on the 'Partial' Larvae of Sphaerechinus," *Archiv für Entwickelungsmechanik der Organismen, 2* (1895), 123.

42. T. H. Morgan, "Regeneration of Tissue Composed of Parts of Two Species," *Biol. Bull., 1* (1899), 7-14. Morgan's interest in Born's grafting techniques may have been influenced by Harrison.

43. T. H. Morgan, "Regeneration: Old and New Interpretations," *Biol. Lect.*, 1899 (1900), 185-208.

sex determination.[44] Yet while Conklin continued to consider causes of differentiation and while Wilson began to study the nucleus to find explanations of differentiation, Morgan became increasingly interested in the embryonic processes of establishing or determining the differentiated form. The results of his comparisons of normal and abnormal development in frogs, besides producing a description of development, led him to conclude that development depends on physiological contractile processes. By 1907 he was emphasizing the "role of irritability and contractility as dynamic factors in development and regeneration."[45]

Rather than concentrating on the morphogenetic problems of when and where differentiation occurs, which he had earlier considered, he felt that it was more productive to study how, once the "formative influence" has been established, actual formation progresses. This study involved the vague area in which morphology and physiology overlap, Morgan recognized, a fact that illustrates the misdirectedness of our attempting, as historians, to divide biology into such neat differentiated categories as morphology and physiology. As Morgan wrote:

> Morphogenesis does not express my meaning in all respects, for I am not concerned so much with changes in form as with the rate of growth and of differentiation. If I have taken a liberty in using the term physiology to cover these kinds of changes, my excuse must be that we are dealing with phenomena that lie on the borderland, where physiology and morphology overlap, and appear to merge into each other.[46]

Assumptions, commitments, and definitions were changing between 1890 and 1910.

In 1908, Morgan continued to emphasize the role of the forces in

44. T. H. Morgan, "Recent Theories in Regard to the Determination of Sex," *Pop. Sci. Monthly, 64* (1903), 97-116; and Morgan, "The Biological Significance and Control of Sex: Sex Determining Factors in Animals," *Science, 25* (1907), 382-384.

45. T. H. Morgan, "The Relation between Normal and Abnormal Development of the Embryos of the Frog as Determined by Injury to the Yolk-Portion of the Egg," part I, *Archiv für Entwickelungsmechanik der Organismen, 15* (1902), 283-313, through part X, *19* (1905), 588-614, esp. p. 612 of part X; Morgan, "The Role of Irritability and Contractility as Dynamic Factors in Development and Regeneration," in *Seventh International Zoological Congress, 1907* (Cambridge, Mass., 1910), pp. 1-8.

46. T. H. Morgan, "The Physiology of Regeneration," *J. Exp. Zool., 3* (1906), 457.

the egg, which could also be influenced by external conditions. Neither egg stratification, nor the cleavage planes, nor the nucleus seems to determine such things as bilaterality, Morgan maintained; so physiological processes must be essential. In 1909, Morgan reached a turning point. He reported that his work "led me to abandon the hope of finding a clue to *sex determination* in the external conditions, however important these factors may be in cyclical changes in *sex production* . . . The discovery at the same time of an internal mechanism *associated* with sex determination has gradually brought conviction that internal and not external factors determine sex."[47] Thus, like Wilson, Morgan was led, reluctantly at first, back to the nucleus; his work of 1909 and after began to reveal his growing conviction that the causes of differentiation were after all internal.

Still concerned with what determines differentiation and what forces shape development, Morgan refocused his studies to achieve productive results. He continued to try to unite his concern with factors of differentiation and with the later expression of determination (witness *Embryology and Genetics* published in 1934)[48] as he tried to discover the respective roles of genetic material and protoplasmic material in development. While he maintained his original concerns, Morgan's changing emphases continued to move him gradually along the continua of possible scientific commitments in the direction of further experimentation, narrower questions, and more definite results. But again, despite his later vocal endorsement of experimental biology, there is no evidence of a revolt against the old concerns and methodological commitments; rather, new emphases evolved, and commitments and assumptions underwent reshaping until a research program emerged in 1910. It was primarily after 1910 that Morgan saw his experimental program as fundamentally different from even his own earlier descriptive work.

The career of Ross Harrison (1870-1959) was a bit different from that of his colleagues. After receiving his A.B. in 1889 and while completing his Ph.D. (1894) at Johns Hopkins, Harrison also completed an M.D. degree at the University of Bonn. This medical interest separates him from his fellow Johns Hopkins graduates and helps to explain his

47. T. H. Morgan, "A Biological and Cytological Study of Sex Determination in Phyloxerans and Aphids," *J. Exp. Zool.*, 7 (1909), 239-352.

48. T. H. Morgan, *Embryology and Genetics* (New York: Columbia University Press, 1934).

different research emphases, which kept him interested in later developmental stages rather than in the earliest stages of differentiation.[49]

Harrison's initial work concerned morphogenesis of teleost fins. Using basic experimental manipulations influenced by Moritz Nussbaum, an experimental anatomist and his advisor at Bonn, Harrison sought to answer questions about what happens and what factors act to direct the development of body parts.[50] In that early work, Harrison became frustrated because he could not detail or explain the complex processes of nerve development. The bulk of his work until 1907 was therefore directed at understanding nerve development, but the particular questions he asked and the methods he employed changed in important ways.

In 1898 Harrison used Gustav Born's method of heteroplastic grafting, in which parts of embryos are transplanted onto other, host, embryos. As Morgan also soon recognized, heteroplastic grafting allows manipulation of organisms and production of abnormal specimens, both of which provide additional data with which data on normal development can be compared. Thus the technique facilitates description of what cells or groups of cells do as they pass through developmental stages. Until 1903-1904, Harrison proceeded with such descriptive studies of later stages of embryonic development, using grafting and other techniques.

In 1903 and 1904, he began to address the various competing theories about nerve fiber development and to produce evidence supporting the neuron theory.[51] After he attended an important meeting in Jena, from 1904 to 1910 Harrison campaigned to make the neuron theory convincing. At the same time he became increasingly

49. For biographies of Harrison, see J. S. Nicholas in *Biog. Mem. Nat. Acad. Sci., 35* (1961), 132-162, with complete bibliography; Jane Oppenheimer, "Ross Harrison's Contributions to Experimental Embryology," *Bull. Hist. Med., 5* (1966), 525-543, and in the *Dictionary of Scientific Biography*.

50. Ross Granville Harrison, "Über die Entwicklung der nicht knorpelig vorgebildeten Skelettheile in den Flosse der Teleostier," *Archiv für mikroscopische Anatomie, 42* (1893), 248-278; and Harrison, "Die Entwicklung der unpaaren u. paarigen Flosen der Teleostier," *Archiv für mikroscopische Anatomie, 46* (1895), 500-578.

51. R. Harrison, "Experimentelle Untersuchungen über die Entwicklung der Sinnesorgane der Seitenlinie bei den Amphibien," *Archiv für mikroscopische Anatomie, 63* (1903), 35-149; and Harrison, "Neue Versuche u. Beobachtungen über die Entwicklung der peripheren Nerven der Wirbeltiere," in *Sitzungsberichte d. Niederrhein Gesellschaft f. Natur u. Heilkunde* (Bonn, 1904), pp. 1-7.

concerned with describing and explaining the dynamic causes of embryonic development more generally.

As has been established elsewhere, Harrison's methodology changed in subtle ways during this period.[52] After beginning with traditional experimental manipulations and preparation techniques, he adopted increasingly sophisticated experimental methods, at first with the hope of providing a convincing, or "crucial" proof of the neuron theory. Later, by 1910, he recognized the futility of producing a proof, but he established his point convincingly by embedding his research results within an institutionally based research program demonstrated to be promising.[53] Harrison's sense of what research ought to be like had changed by 1910, so that he then articulated a particular experimental approach and problems.

Because Harrison was concerned with differentiation of body parts rather than individual cells in the earlier cleavage stages, and with the way in which differentiation of those parts becomes determined (that is, is not reversible), he concentrated on different questions and different research materials than did Wilson, Conklin, or Morgan. Yet he became the institutional leader for the emerging shared emphasis on using experimental manipulations and comparative studies of manipulated abnormal development when Wilson, Conklin, and Morgan chose him as the managing editor of the *Journal of Experimental Zoology* in 1904.[54] In his work, he exemplified a gradual move along the continua toward experimental biology, asking narrow questions, and achieving specific and definite results. Like Wilson's, Conklin's, and Morgan's, Harrison's shifting assumptions about science led him by 1910 to articulate a specialized and productive research program. But like the others, too, Harrison took the years 1890-1910 to redefine and reshape, gradually, what he wanted his science to do.

CONCLUSION

Despite their individual differences, the four Americans studied here are striking in their similarities. Perhaps influenced by William Keith Brooks's emphasis on being familiar with current publications, each became aware of the proliferation of contradictory themes about individual development. In the shared desire to make sense out of this confusion, each came to believe that rather than more speculative theories, what was needed was more data – descriptive, comparative, and experimentally derived data – and more careful consideration of those data. Then, each decided that the problem of describing and explaining differentiation was too large. For productive results, which each man had come to value as an essential part of his science, it was necessary to ask narrower questions for which relevant data could be found. Influenced by the German ideal of the research *Institut*, specialized research programs emerged by 1910 as each individual worked through his assumptions. Wilson became a cytologist, Morgan a geneticist, Conklin an evolutionary embryologist with broad research interests, and Harrison an experimental embryologist. Reference to continua of possibilities rather than dichotomies has allowed me to illustrate that these programs emerged gradually and continuously.

Yet even though embryology in 1910 was not incommensurable or essentially in conflict with that of 1890, the newer science was nonetheless manifestly different from the older. It might seem, therefore, that such a drastic change must have involved a revolution, or what might as well be called a revolution in at least the non-Kuhnian sense of radical change (which, as I have explained, is what many historians mean by revolutionary science). Why not admit that a rapid change is a revolution and that biology thus changed discontinuously, one might well ask?

To call the changes between 1890 and 1910 revolutionary or to stress the speed or discontinuities of scientific change, I feel strongly, distorts the essence of this period in biology. It is precisely the gradual and continual reworking of assumptions and the concern with developing new research efforts based on the old that characterizes turn-of-the-century embryology. Research developed in new directions that supplemented and replaced the old, but before 1910 the Americans did not see their task as revolting against or rejecting earlier biology. Rather, they sought to break down old antagonisms and disputes among naturalists and physiologists on subject matter and method. They sought to combine manipulative/laboratory methods, medical problems, evolutionary concerns, and field interests. Thus calling their work revolutionary suggests something more than actually occurred for the individuals involved in this case.

52. See Jane Maienschein, "Ross Harrison's Crucial Experiment as a Foundation for Modern American Experimental Embryology," Ph.D. diss., Indiana University, 1978.

53. R. Harrison, "The Outgrowth of the Nerve Fiber as a Mode of Protoplasmic Movement," *J. Exp. Zool.*, *9* (1910), 787-846. See Maienschein, "Ross Harrison's Crucial Experiment," for discussion of the institutional and sociological factors involved.

54. "Facsimile of First Announcement of the J.E.Z." and "Retrospect, 1903-1945," *J. Exp. Zool.*, *100* (1945), vii-xxxi.

Yet to call this episode of scientific change evolutionary also invokes a misleading analogy. The *emergence* of individual programs *was* essentially gradual for the researchers involved. But *acceptance* of the new programs, especially after 1910, involved vocal and self-conscious rejection of older work. The programs were perceived by new participants as offering something exciting and essentially different from, if not incommensurable with, the older work. Indeed, the complex of assumptions of the new work is, as a whole, quite different from the complex of the older work, as is revealed by analysis of the shifting assumptions along the various continua. In sum: shifts in *individual* assumptions necessary for the emergence of programs seems gradual and relatively continuous, while shifts in acceptance from the older programs to the newer appear relatively rapid and discontinuous (though still not revolutionary in Kuhnian terms). Whether a more continuous or more discontinuous view is more appropriate therefore depends on one's focus.

As a result, quibbling about whether to call scientific change in general evolutionary or revolutionary, continuous or discontinuous is misguided. Instead of endorsing either an evolutionary or a revolutionary historical position, I argue for an awareness of the range of possible methods, ontologies, theories, and goals. These continua prove useful for showing how relatively gradual or more rapid change has been where the change is continuous or discontinuous, and in what direction change has occurred – for individual scientists and for research programs both. Like the biologists in question, I am stressing the need for accurate data and careful comparative discussions, using whatever techniques are productive, but with awareness of the range of possibilities rather than dichotomized views.

The result for the historian of science, I hope it is obvious, will be to facilitate a more accurate picture of what actually happened in the past, of the way scientific ideas have changed for both individuals and for groups. But the use of continua of possible assumptions about science does not simply reveal what science was and how science did change in the past; the complex of continua should also be useful for illuminating what science is and how science changes generally, which are, after all, issues of concern for both historians and philosophers of science.

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