Cell Lineage, Ancestral Reminiscence, and the Biogenetic Law

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Before 1859 most embryologists explained the development of individual organisms in terms of conformity to a species type. After 1859, the appearance of evolution theory meant that this type-explanation could no longer adequately account for individual development because the types no longer existed. According to the evolutionary viewpoint, since an individual had a complex evolutionary past, it might well have inherited "information" from distant ancestors as well as from its parents. Evolutionists accepted that ancestral factors from the evolutionary past might condition an organisms's development, an idea which led to the corresponding notion that the study of individual development could delineate ancestral evolutionary relationships.

This relation of the individual developing organism to its ancestral evolutionary past found expression in the "biogenetic law," which states that "ontogeny is a rapid and shortened recapitulation of phylogeny." Having first gained popularity through its statement by Ernst Haeckel in 1866, the recapitulation idea still appears in modern texts and is familiar to today's high school biology student.[1] Today, biology still deals with biogeny, or the history of the evolution of living things, and hence considers similarities and differences between individuals and their ancestors. However, biologists no longer regard ontogeny as repeating phylogeny in a uniform way which can be captured by a law. The meaning of the relation has changed significantly since 1866.

I propose to discuss one of the many factors responsible for this shift in understanding. Six Americans, C. O. Whitman, E. B. Wilson, E. G. Conklin, A. L. Treadwell, A. D. Mead, and F. R. Lillie, studied in detail the earliest cellular stages of ontogeny, and their contributions played a transitional role in contributing to the understanding of the ontogeny-phylogeny relation. Their cell-lineage studies replaced

1. The idea appears in several places in Ernst Haeckel's *Generelle Morphologie der Organismen* (Berlin: G. Reimer, 1866). It is also expressed in such modern works as B. I. Balinsky's *An Introduction to Embryology* (Philadelphia: W. B. Saunders, 1970), pp. 9, 590.

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Haeckel's understanding as stated in his biogenetic law with a modern interpretation of the relation. In this paper I will sort out the relative contributions of each man in order to understand better the transitional role which they played together. I do not claim that these men were responsible for a general acceptance of our modern understanding of the recapitulation idea. Rather their work reflects their own emerging understanding of the relation of individual development to that of the individual's ancestors.

HISTORICAL CONTEXT

The recapitulation idea brings together the two separate problems of individual development and of species development, the concerns of embryology and evolution, respectively. Embryology must account for the process of embryonic differentiation into organs and parts; Karl Ernst von Baer raised the problem of embryology in its modern form in the General Scholia of his major work.[2] E. S. Russell and Jane Oppenheimer have both discussed von Baer's embryological contributions in some detail and have made it clear that von Baer subscribed to a type-concept of species and to an epigenetic view of development.[3] Von Baer saw individuals as developing according to their species type, with the typical characters emerging gradually and successively. This gradual unfolding of the species form which is development occurs first in the germ layers, then continues in the transformation of those germ layers into organs and parts. Von Baer concerned himself with describing ontogeny and with using ontogeny to classify forms; he did not consider ontogeny's relation to phylogeny because for him there was no phylogeny. The idea of phylogeny, which requires historical generation of phyla and species, something that was impossible within von Baer's system of static types, appeared only later with Darwin, and the word itself did not appear until Haeckel used it.[4]

With the *Origin of Species* in 1859, Charles Darwin introduced the idea of species development according to which any given individual has

2. Karl Ernst von Baer, *Über Entwickelungsgeschichte der Thiere* (Königsberg: Bornträger, 1828), part 1.

3. E. S. Russell, *Form and Function* (London: John Murray, 1916), chap. 9; Jane Oppenheimer, *Essays in the History of Embryology and Biology* (Cambridge, Mass.: MIT Press, 1967), esp. pp. 141-147, 295-307.

4. *The Compact Edition of the Oxford English Dictionary* (1971). Though Darwin did not use the word *phylogeny* in the first edition of the *Origin* his meaning was the same.

ancestors from a number of historically related species. With the advent of the theory of evolution, therefore, the problem of individual development became linked to the historical problem of species development. Darwin elaborated upon this relationship. One of his goals was to establish a natural classification system for species by tracing genetic lines of descent through embryology,

> Descent being on my view the hidden bond of connexion which naturalists have been seeking under the term of natural system. On this view we can understand how it is that, in the eyes of most naturalists, the structure of the embryo is even more important for classification that that of the adult. For the embryo is the animal in its least modified state; and in so far it reveals the structure of its progenitor. . . . Thus the community of embryonic structure reveals the community of descent. It will reveal this community of descent, however much the structure of the adult may have been modified and obscured.[5]

Hoping that ancestral connections could be traced with the help of embryology, Darwin nevertheless urged that "it should also be bourne in mind, that the supposed law of resemblance of ancient forms of life to the embryonic stages of recent forms may be true, but yet, owing to the geological record not extending far enough back in time, may remain for a long time, or for ever, incapable of demonstration."[6]

Disregarding this caution, Ernst Haeckel enthusiastically took up Darwin's suggestion that present embryonic forms hold the key to phylogenetic relationships. In fact, Haeckel assigned to embryology a far greater role in evaluating those relationships than Darwin had. Incorporating an idea from Fritz Müller's *Für Darwin* of 1864, Haeckel stated that "ontogeny is a brief and rapid recapitulation of phylogeny," or in other words:

> The History of the Evolution of Organisms consists of two kindred and closely connected parts: Ontogeny, which is the history of the evolution of individual organisms, and Phylogeny, which is the history of the evolution of organic tribes. Ontogeny is a brief and rapid recapitulation of Phylogeny, dependent on the physiological functions of Heredity (reproduction) and Adaptation (nutrition).

5. Darwin, *Origin of Species*, 1859 ed., p. 449.
6. Ibid., p. 450.

> The individual organism reproduces in the rapid and short course of its own evolution the most important of the changes in form through which is ancestors, according to the laws of Heredity and Adaptation, have passed in the slow and long course of their paleontological evolution.[7]

According to Haeckel embryos pass in the course of development through forms which correspond to the adult stages of their evolutionary ancestors. Yet only with the gastrula is the form morphologically significant respecting the formation of future organs – which Haeckel considered critical. Only when the germ layers are formed in the gastrula is there morphological differentiation in Haeckel's view, and thus the recapitulation idea relies on the germ-layer theory. Before gastrulation all cells are homogeneous. Actually, Haeckel pointed out that this last statement must be modified: there may be visible minor differences between cells before germ-layer formation. These premature differences occur, however, only in "coenogenetic" organisms which have diverged through adaptation from the ancestral pattern of development. His "palingenetic," or truly ancestral, ontogeny involves strictly vegetative divisions of the egg protoplasm into numerous cells up to the gastrula stage.

For Haeckel ontogeny is *caused by* Phylogeny. The fact that a phylogeny contains particular adult forms actually makes it causally necessary that the embryo will assume those forms progressively during its ontogeny. For Haeckel phylogenetic history provides a sufficient cause and a sufficient explanation of the particular course of development through which an individual passes.

Haeckel found embryology primarily interesting not in itself but as a tool for understanding evolution, useful in drawing up phylogenetic trees for each organism. Haeckel's materialism and his phylogenetic causality were extreme, going beyond what is contemporaries were willing to accept.[8] The most significant opposition to Haeckel's program came from several outspoken zoologists who accepted evolution

7. Müller, *Facts and Arguments for Darwin* (London: John Murray, 1969), p. 100. Müller is regarded as a forerunner of Haeckel, but his views are much more cautiously expressed than Haeckel's. Haeckel's "law" is stated throughout his own works, especially in *Generelle Morphologie*, and *Evolution of Man* (New York: Appleton, 1879; first German ed., 1874), esp. pp. 1-2. Haeckel's views are also summarized in Russell, *Form and Function*, pp. 247-260.

8. Oppenheimer, *Essays*, pp. 209-213; Russell, *Form and Function*, p. 259.

but rejected what they regarded as Haeckel's perversion of embryology for evolutionary purposes. Wilhelm His was one of these men.[9]

In 1874 His published a series of letters to his nephew under the title *Unsere Körperform und das physiologische Problem inhrer Entstehung.*[10] In that work His opposed Haeckel's program, arguing that construction of phylogenetic trees is not a proper goal for embryology. Embryology ought to seek explanations of development, and in His's view phylogeny does not explain ontogeny. His's embryology would explain individual development in physiological terms, as a function of direct and indirect factors which may operate on the embryo either internally or externally. In his account, form begins with the germ, then develops epigenetically according to the complex laws of growth and differentiation. Though His did not specify precisely what these laws are and therefore left his program for a physiology of development on rather indefinite ground, he did outline factors of development which he felt provided the foundation of ontogeny and a key to understanding development.[11]

His rejected Haeckel's program of tracing phylogenies. His views differed from Haeckel's in emphasizing the problem of individual development in its own right. Thus His regarded the differences, however subtle, in embryos as more significant than the superficial similarities which Haeckel emphasized. Basically, His returned to von Baer's concern with accounting for the emergence of differentiated form, but he phrased his problem and proposed his solutions in mechanical terms, as von Baer had not, asking how material factors and forces result in the observed developmental processes. In seeking an explanation of ontogeny His turned away from Haeckel's preoccupation with evolution and placed emphasis on the developing individual organism, which happens also to be a product of evolution.

Wilhelm Roux was the most highly visible of the proponents of His's program during the 1880's and 1890's, as he extended, elaborated, and progagandized the call for a mechanical understanding of development. Going beyond His, he called for the use of controlled experimentation in embryology, but like His, his primary goal was to understand the mechanical laws of development itself. Roux, like His, rejected

9. His is important both because he was an excellent and highly regarded zoologist and because he had a well-publicized feud with Haeckel.

10. Wilhelm His, *Unsere Körperform . . .* (Leipzig: Vogel, 1874).

11. See ibid., pp. 174-175, for an outline of the factors His considered relevant.

Haeckel's biogenetic law.[12]

Besides these well-known individuals, there were several American embryologists whose important role in bringing together purely embryological and evolutionary problems has been largely overlooked by historians. Each of these Americans, Whitman, Wilson, Conklin, Treadwell, Mead, and Lillie,[13] accepted that ontogeny and phylogeny are in some way related, although they did not accept the causal necessity which Haeckel's biogenetic law required, and they moved away from the germ-layer emphasis in development to a concern with cells. Out of their combined efforts came a new understanding of the relation of individual to species development. From their studies also came the view that the differences between two closely related ontogenies are as important for embryology and as worthy of investigation as are the similarities which Haeckel had emphasized. From the work of these men emerged an understanding of the embryo as a complex product of inherited developmental information which tended to be conservative of the parental form and at the same time responsive to constant adaptations to changing environmental conditions. These men saw phylogenies as series of adult forms which might imperfectly reflect ancesttral ontogenies but which, in contrast to Haeckel's view, could in no way cause ontogeny. While rejecting the causal relation of phylogeny to ontogeny that is part of Haeckel's law, each member of the group partook of the shared effort to discover and articulate what that relation was. Frank Lillie articulated in 1908 the understanding toward which these men seem to have been moving. Lillie's was perhaps the first clear statement of the modern view of ontogeny-phylogeny relations, and I shall return to a discussion of his work later.

THE CELL-LINEAGE RESEARCHERS

Before dealing with each individual in turn, it is important to explain why I consider them here as a group. Charles Otis Whitman (b. 1842) was the inspirational leader and influenced each of the other five men, Wilson (b. 1856), Conklin (b. 1863), Treadwell (b. 1866), Mead (b. 1869), and Lillie (b. 1870). Each of these men worked in contact with Whitman at the Marine Biological Laboratory (MBL) at Woods Hole,

12. Whilhelm Roux, "Kritische Referat" (1886), in *Gesammelte Abhandlungen* (Leipzig: W. Engelmann, 1895), I, 443-447.

13. These six are the major figures; there were also several others, such as F. M. Surface and S. J. Holmes, who contributed factual information.

Massachusetts. All performed cell-lineage studies, which were exact studies of what happens to each blastomere of a developing egg in the course of early cell divisions. All published major cell-lineage papers in the *Journal of Morphology*, which Whitman had established in 1888. During the summer Friday night lecture sessions at Woods Hole they all presented lectures, and these papers subsequently appeared in the *Biological Lectures* of the MBL. Each man mentioned the others in his published works and each built on the preceding studies of his fellow investigators. These men knew of each other and of each other's work, and many remained for years in close personal contact, though the extent of that contact is not clear in each case. Given the fact that all were undertaking comparative studies, it is unlikely that any one man would have been successful without the valuable interaction which helped considerably to clarify issues. On these grounds it seems quite legitimate to consider Whitman, Wilson, Conklin, Treadwell, Mead, and Lillie together.

Each of these men was concerned both with explaining the development of individuals and with elucidating evolutionary relationships between organisms.[14] Each considered Haeckel's goal of establishing phylogenetic relationships important, but came to regard His's search for a physiology of development as more critical. It seems that these men were not fundamentally motivated by Roux in their cell-lineage studies and that they were not strict followers of Roux's program of experimental *Entwickelungsmechanik*, as Garland Allen has suggested.[15] They were motivated by their own interests in both development and evolution, stimulated by His and, except for Whitman himself, inspired by Whitman. They were trying to establish the twofold nature of development. For this they considered, first, the extent to which each individual embryo is a historical being and is therefore primarily reminiscent of its ancestors because it is the result of past evolutionary change and, second, the extent to which an individual embryo is actually subject to external pressures and adaptive at every stage of its development. In both cases the individual organism is a product of natural selection. The difference lies in whether the selective pressures on embryos have operated in the past or are still operating in the present.

Of the six men each contributed to the new understanding of the

14. At least this was true in the 1890's and early 1900's, though these men changed their interests and their views as time and the state of biology progressed.
15. Garland Allen, *Life Science in the Twentieth Century* (New York: Wiley, 1975), esp. pp. 34-35.

ontogeny-phylogeny relation which Lillie articulated. Though each was unique in his interpretations and though each went his own way in the early 1900's. moving beyond the cell-lineage studies of the 1890's, all were and continued to be concerned with the issues outlined above. It will be worthwhile to consider each of these men in turn in order to appreciate the emergence of Lillie's statement of the biogenetic relationship, for Lillie built upon the foundation created by the work of the others as well.

C. O. Whitman

As mentioned, Charles Otis Whitman may be considered the "inspirational head" of the American embryologists who studied cell lineage. Whitman had taken advantage of the best opportunities for an aspiring zoologist of his time. He had attended lectures at Louis Agassiz's Anderson School on Penikese Island, had worked at the Naples Zoological Station, and had studied under Rudolph Leuckart in Leipzig. Shortly after returning to the United States he became a professor at Clarke University and then at the University of Chicago. Perhaps most important for my study was his assumption in 1888 of the first directorship of the newly-formed MBL. Until his death in 1910 he remained an active force in establishing the strength and reputation of that independent institution. It was there that the others came into contact with Whitman. He has been called by Edward Morse in the National Academy of Science *Biographical Memoirs* "a genius, honorable and truth-loving," and the tributes paid him by his students attest to his impressive and motivating presence.

In 1878 Whitman's "The Embryology of Clepsine" appeared.[16] This was the first cell-lineage study, and in initiating emphasis on following early cells and cell divisions through development, Whitman turned away from Haeckel's concern with the later germ-layer stages. Whitman's paper traced the development of each individual blastomere from the one-cell unsegmented egg stage to the gastrular, germ-layer stage. Working with the leech *Clepsine*, an annelid, Whitman concluded that these earliest stages were significant morphologically, that the early cell divisions were not simply quantitative vegetative divisions as Haeckel thought but that they were qualitative differentiations as well. This conclusion opposed Haeckel's view that only the germ layer and later

16. C. O. Whitman, "The Embryology of Clepsine", *Quart. J. Micro. Sci., 13* (1878), 215-315.

stages held qualitative importance for differentiation in individual development. With this paper Whitman expressed doubts about aspects of Haeckel's embryological study, but he did not reject Haeckel's entire approach. Whitman seems to have accepted in 1878 at least the search for phylogenetic relationships as a legitimate embryological concern.

Whitman's paper of ten years later, "A Contribution to the History of the Germ-Layers in Clepsine,"[17] set the pattern for studies of cell lineage. Appearing in the first issue of the *Journal of Morphology*, this study begins with a detailed description of the earliest stages of development to the formation of the germ layers in *Clepsine*. It then proceeds to a discussion of "Special and General Questions," in which Whitman asks whether the trochophore stage (a free-swimming larval stage through which some marine annelids pass) is primary and ancestral or whether it is secondary and adaptive, in which case a more direct fetal development would be primary. At issue was the phylogenetic significance of the annelid larva. If the larval form of annelids was secondary, then the larva would not conform to a phylogenetic ancestor and could be explained as an adaptation to environmental conditions which had changed since the ancestors had lived. But if the larval form was primary, then there would be two possibilities. Either Haeckel was right and there must be an evolutionary ancestor of the annelids corresponding to the larval stage or Haeckel's recapitulation theory must be incorrect. Drawing on his studies of early cell lineage in *Clepsine*, Whitman concluded that in fact the trochophore, or separate larval stage, was primary. He felt that it was derived from a primitive gastrula and was not a secondary adaptation. *Clepsine*, which has no trochophore stage, actually follows an adaptive, or fetal-type, development in which the appearance and location of the blastopore are altered from the primary or ancestral pattern, as exemplified in the related species, *Polygordius*, with its larval development.[18]

Albert Davis Mead contributed to this discussion primarily on the factual level, compilling more and varied cell-lineage studies on which Whitman and the others could draw for comparisons. Mead began work at the MBL somewhat later, in 1891, by comparing a variety of forms, mostly gastropods and annelids, to study homologies and to postulate genealogical relationships. Mead placed particular emphasis on the adaptive value of the trochophore larval stage of annelid development,

17. C. O. Whitman, "A Contribution to the History of the Germ-Layers of Clepsine," *J. Morph.*, *1* (1888), 105-182.

18. Ibid., pp. 172-177.

but seems to have constructed no fully articulated theory of development based on that work. He did maintain that trochophore development, with homologies in the origin and fate of prototrochal cells, strengthened the supposed relation of annelids and mollusks that related to Whitman's work of 1878.[19]

Although Whitman did not address Haeckel's biogenetic law directly, in his discussion he was concerned with phylogenetic relations. But moving beyond Haeckel's phylogenetic concern, Whitman was also, and primarily, raising the questions of precisely how an individual develops and what processes are involved in annelid formation. He was concerned more with His's question than with Haeckel's, but considered both. This dual concern was not in itself unique, but Whitman's particular theories did move his work in a direction beyond both Haeckel and His.

Though Whitman carefully avoided articulating an explanation of development, which he felt would necessarily be incomplete, he did raise important issues. For example, he did not believe that the hereditary "information" which transmitted ancestral adaptations resided exclusively in the nuclear chromosomes, as had been argued by Haeckel and Roux. Rather he felt that "the egg is from the beginning of its existence as an individual cell definitely oriented."[20] This view raised the possibility that organs and parts were generated directly from predetermined areas of the egg by internal factors of development only. There need be no external factors to stimulate differentiation if the egg was already to a degree differentiated. Whitman realized that the distiction between the roles of internal and external factors was far from clear as yet, and he felt that one new goal for embryology was precisely to define those relative roles. If the developing organism was guided only by internal differentiation, then development would be strictly according to the ancestral pattern, which was inherited; if external factors prevailed, then adaptations to present conditions would be most important. In Whitman's view natural selection held explanatory power and could explain development. He believed that adaptations to past conditions, which were inherited and operated internally, were important, but that ongoing changes due to present conditions, which operated by acting on the embryo with external pressures, also played a role in development.

19. A. D. Mead, "The Early Development of Marine Annelids," *J. Morph.*, *13* (1897), 227-326; and Mead, "The Cell Origin of the Prototroch," *Biol. Lect.*, 1898, pp. 113-138.

20. C. O. Whitman, "Evolution and Eoigenesis," *Biol. Lect.*, 1894, pp. 205-224.

Whitman was never very explicit about his own theories, and it is difficult to ascertain exactly what he understood the relations of ontogeny to evolutionary ancestors to be. It is clear that he saw ontogeny as a complex process which involved internal and perhaps external influences and which was guided by the regulatory power of the organism as a whole, but he seems not to have sorted out the precise roles which inherited and adaptive factors play – a critical distinction for a modern understanding of ontogeny. Nonetheless, besides initiating the fruitful study of cell lineage, he also moved away from Haeckel's postulated causal necessity and raised the problem of ontogeny as a product of evolution in a way which his followers could develop further. This was his conceptual contribution to the eventual rewriting of the biogenetic relation of ontogeny to phylogeny.

E. B. Wilson

Edmund Beecher Wilson began his embryological career before he worked with Whitman; he studied under William Keith Brooks, a proponent of Haeckel's views, at the Johns Hopkins University from 1878 to 1881. Wilson's first papers of 1878-1882 were primarily systematic descriptions of various invertebrate species and their corresponding ontogenies.[21] His first significant paper, "The Development of Renilla," appeared in 1883 and traced the embryology of these sea pansies, from a genus of marine colonial polyps.[22] Though this study dealt with early cleavage, it focused on the germ layers and the formation of later emerging organs. Throughout his paper Wilson did not explicitly endorse or reject Haeckel's biogenetic law and the emphasis on germ layers and later development which accompanied that law. Although he may very well have considered the issue, Wilson gives no evidence that he had yet seriously questioned or rejected either the law or the germ-layer emphasis.

To some extent Wilson had begun to recognize the inadequacies and confusions of tracing evolutionary relationships by 1890, when he gave

21. For a list of Wilson's early works see *N.A.S. Biog. Mem., 21* (1941), 336-342, and Alice Baxter's Ph.D. diss. "Edmund Beecher Wilson and the Problem of Development: From the Germ Layer Theory to the Chromosome Theory of Inheritance," Yale University, 1974. The latter includes extended discussion of many of the early works. An extract appears in "Edmund B. Wilson as a Preformationist," *J. Hist. Biol., 9* (1976), 29-57, of which pp. 39-48 are most relevant.

22. E. B. Wilson, "The Development of Renilla," *Phil. Trans. Roy. Soc. London, 174* (1883), 723-815.

a lecture entitled "Some Problems of Annelid Morphology."[23] After pointing out that annelid development is important for understanding vertebrate development because of critical similarities, he cautioned that much of the theorizing to date proved far from convicing. In particular, he cited the trochophore and especially the origin of its mesoblast (the middle germ layer) as problematic. The trochophore of *Polygordius*, for example, could be interpreted as being primary and ancestral or as being secondary and adaptive, as Whitman had discussed. In opposition to Whitman, Wilson expressed a somewhat hesitant preference for the latter view and thereby denied the value of the trochophore for evaluating ancestral phylogenetic relationships. Resolution of such debates requires facts, Wilson urged, not further theorizing. While not yet denying the value of pursuing evolutionary relationships through gross comparisons of the germ layers, Wilson clearly recognized problems with that search because of the ambiguities in interpretations of empirical data. This paper shows that Wilson was still operating within an essentially Haeckelian context, considering phylogenetic questions through germ-layer studies. Yet it also demonstrates that at this point he felt frustrated by the confusions of the search and sought the more stable ground of empirical detailed description of embryonic development.

By 1892 Wilson had rejected much of Haeckel's idea of recapitulation and the priority given to evolution which it involved. By the time his classic work on the annelid worm *Nereis* appeared in 1892, Wilson had studied at Cambridge, in Germany, and at the Naples Zoological Station. Also, significantly, in the summer of 1891 he had worked at the MBL, where he had come into contact with Whitman while he was studying the night-crawling *Nereis*, which was quite abundant in the Wood Hole area. In the 1892 paper which resulted from that study Wilson took an implicit stand against Haeckel's statement of the biogenetic relation.[24] Concentrating on early cell lineage up to the trochophore stage, Wilson stated that ontogeny is more like a series of organogenies in which each organ begins from a single blastomere, and is better viewed from an individual and ontogenetic rather than a phylo-

23. E. B. Wilson, "Some Problems of Annelid Morphology," *Biol. Lect.*, 1890, pp. 53-78.

24. E. B. Wilson, "The Cell-Lineage of Nereis. A Contribution to the Cytogeny of the Annelid Body," *J. Morph.*, 6 (1892), 361-480. His opposition was directed against a statement by Kleinenberg in particular but was also opposed to Haeckel's inaccuracies.

gentic point of view. Generalizing from the case of *Nereis* by comparing his own with other cell-lineage studies of annelids and mollusks, Wilson concluded that the developing organism resembles a cleavage mosaic in which the material of the egg is divided early according to its later role. He saw the early blastomeres as already having morphological significance for adult parts which were to emerge later, but recognized that the pattern may also be regulated later by the needs of the whole organism as it responds to its particular environmental conditions.

Wilson maintained that development is not strictly an unfolding of form according to mechanical principles and present conditions, for there is an evolutionary factor, an ancestral component, which must be considered as well. Comparing polyclade development with annelid and mollusk development shows how these factors lead to different results in different organisms. The divergence of these organisms

> is a fact of capital importance, for its proves that cells having precisely the same origin in the cleavage, occupying the same position in the embryo, and placed under the same mechanical conditions, may nevertheless differ fundamentally in morphological significance. We cannot escape the conclusion that the cell possesses a definite hereditary tendency upon which primarily its nature depends, however much its outward form or mode of division may be affected by the mechanical conditions of its environment in the body; and full weight must be given to this heredity in every attempt to interpret the origin and meaning of cleavage-forms.[25]

Wilson thus emphasized that the developing organism is partially a product of an evolutionary past. Yet he showed that while each cell has its "hereditary tendency," the development of the whole organism is regulated by the present needs of that whole, because no cell is isolated from its organismal surroundings. It is not simply the sum of individual cells, acting like pieces of a mosaic, which results in successful development and characteristic differentiation. There are two factors controlling development in Wilson's view: the hereditary of ancestral tendency and the regulatory or present adaptive tendency. Wilson hoped that an estimation of the relative roles of each would be attained through cell-lineage studies.

After several papers concentrating on the issue of mosaic development, Wilson presented a lecture at the MBL entitled "The Embryolo-

25. Ibid., p. 441.

goical Criterion of Homology."[26] That paper again reflected Wilson's concern with development as a combination of hereditary ancestral factors and adaptive factors. In the paper Wilson drew upon empirical research results, especially from cell-lineage studies, to reach his generalizations. Because homologies were so widely used in establishing phylogenetic and taxonomic relationships, the proper criterion of homology was an important issue. Two primary views of homology prevailed: the embrvological view, which designated homologies not only in structure but also in origin of that structure from the germ layers or cells, and the anatomical view, which maintained a strictly structural criterion of homology.[27] As Wilson pointed out in his paper, by the 1890's the embryological criterion of homology had replaced the anatomical. This was unfortunate, he felt, because the embryological criterion was too closely associated with germ-layer and recapitulation theory, and

> For twenty years embryological research has been largely dominated by the recapitulation theory; and unquestionably this theory has illuminated many dark places and has solved many a perplexing problem that without its aid might have remained a standing riddle to the pure anatomist. But while fully recognizing the real and substantial fruits of that theory, we should not close our eyes to the undeniable fact that it, like many another fruitful theory, has been pushed beyond its legitimate limits.[28]

Also, Wilson maintained, because of lack of information for interpreting embryological data unambiguously, comparative morphology rather than comparative embryology should provide the key to homology. At present the adult form must be the guide by which homologies and thus biological relations are assessed, Wilson believed. He called for careful comparative studies of morphology, from the one-celled ovum upward, to provide a trustworthy basis for a new criterion of homology which would bring together anatomical and embryological information. This new criterion would not be simple or obvious, Wilson pointed out, for adult structural homologies may not have identical origins in the germ layers or cells.

26. E. B. Wilson, "The Embryological Criterion of Homology," *Biol. Lect.*, 1895, pp. 101-124.

27. Russel, *Form and Function*, discusses these criteria of homology in chap. 10 especially.

28. Wilson, "Embryological Criterion," p. 103.

It is true, Wilson held, that homologies, which are manifest only later in development, must be potentially represented in the egg cytoplasm in the sense that the cytoplasm holds all material which will give rise to homologous parts. Yet in the egg those homologies which will later become complete or definite need not be complete or definite. A complete or definite homology would have the same embryonic pattern giving rise to the same adult structures in different organisms; an incomplete homology would have variations in embryonic pattern but the same adult structures. Homologies, which appear in the adult, may not exist in the egg at all, but may emerge only later during the ontogenetic process, because environmental conditions may have altered early development. Thus for Wilson, one task of embryology was to understand how critical external factors may stimulate internal processes to yield adult homologies. This concern reflected his general concern for embryology, to understand how external factors influence inherited internal factors to yield a successful organism.

The study of embryology should involve, according to Wilson, a study of the two factors as set forth by His: the so-called law of growth, which is present in the germ plasm and which represents the essential element of inheritance; and the conditions under which that "law" operates, such as shape and size of the egg, nature of the surrounding medium, and so on. Every development, in other words, is a product of the information for development, which is inherited and internal, and of the environmental conditions, which are external to the germ material, though they may be internal to the organism itself. While His held that development is relatively fixed by heredity, Wilson maintained on the basis of his own cell-lineage studies that environment plays a critical role, hence that ontogenetic processes are far more "plastic" that His had supposed. There are cases in which altered environmental conditions affect development without also altering the end result. These cases demonstrate the plasticity of the developmental process and also show that developmental processes are adaptive rather than strictly ancestral and recapitulatory. Therefore, for Wilson, when heredity appears to have a greater effect on development, this persistence of ancestral conditions, or ancestral "reminiscence," is never simply conservative, continuing even when a characteristic is adaptively useless. Rather "the persistence of ancestral reminiscences in development of homologous parts is in some way connected with the persistence of ancestral conditions of development."[29] Ontogeny is not primarily

29. Ibid., p. 121.

the result of inheritance, with little modification by external factors. Rather, Wilson emphasized the embryo's ongoing response to changes in present external conditions, because *every* ontogenetic stage must have physiological value for the developing individual as it is now, not as it was at some past evolutionary time. Moving away from Haeckel's idea of recapitulation, Wilson delineated the relative roles played by inherited and adaptive factors, by His's "law of growth" and environmental conditions.

The work of Aaron Louis Treadwell is relevant in this regard. Treadwell began work at the MBL in 1891, studying the annelid *Podarke*.[30] His primary interpretive statement held that the resemblances of the early stages in similar organisms had been overestimated by others and that there really are great differences already at the earliest stages. Thus there is less ancestral reminiscence and more adaptation to present conditions. Essentially agreeing with Wilson, Treadwell maintained that homologies have also been overrated for tracing phylogenies as a result of the emphasis on early-stage similarities, for although the cell homology in particular might be useful, it is important to recognize that more homologies are incomplete than are complete. Even where homologies are complete, the origins and subsequent developments of homologous parts in different organisms are only similar and not identical, for according to Treadwell development proceeds as Whitman maintained, regulated at every step by the needs of the organism as a whole. Incomplete homologies may arise when one organism has become adapted in its embryonic development to its particular environment, a situation which causes it to diverge in its embryonic developmental pattern from its closely related species but still to give rise to the homologous part or organ. Treadwell's views did not differ substantially from Wilson's, and his descriptive work lent evidence to Wilson's conclusions.

An 1898 paper by Wilson carried further the issue of inheritance and adaptation in development. Wilson pointed out that a living being maintains an equilibrium between its own parts and its environment and that "the particular character of this adaptation cannot be explained by reference to existing conditions alone, since the organism is a product of the past as well as of the present, and its existing characters give in some manner a record of its past history."[31] It is necessary to sort out

30. A. L. Treadwell, "Equal and Unequal Cleavage in Annelids," *Biol. Lect.*, 1898, pp. 93-111; and Treadwell, "The Cytogeny of Podarke Obscura Verrill," *J. Morph.*, *17* (1900), 399-486.

31. E. B. Wilson, "Cell-Lineage and Ancestral Reminiscence," *Biol. Lect.*, 1898, pp. 21-42, quotation from p. 21.

present adaptive conditions from ancestral reminiscences, or "adaptations which can only be comprehended by reference to former conditions," in order to understand ontogeny and trace phylogenies. Although cell-lineage studies cannot provide definitive proof of ancestral relations, they can serve as a suggestive guide to such relations after the embryologist has sorted out which aspects of development are adaptive and which are ancestral. So far the relations of ontogeny to phylogeny are still not known, said Wilson.

Sometimes, as in the case of the toad, development so completely consists of ancestral reminiscences that it may be regarded as recapitulating the organism's ancestral development or phylogeny, but, as Wilson pointed out, this is quite rare. More often, development is only occasionally and sporadically reminiscent of ancestral embryonic or adult conditions. Reminiscences occur most often in the later developmental stages, but cell-lineage studies show that reminiscences of varying completeness may also occur even at the very earliest stages of cell cleavage (a fact Haeckel had denied). In many animals, such as *Nereis*, cell lineage is well ordered and highly deterministic; thus comparison of related species shows the degree to which species have the same or divergent development. When the species has a high correlation of early to late developmental stages, comparing similarities of early and less complex stages with parallel stages in similar species may provide information about possible phylogenetic relations. One of Wilson's favorite examples concerns the controversial formation of the mesoblast, because comparative study shows that in several species the manner of its formation is closely parallel. Citing work by Treadwell, Conklin, and others, Wilson concluded that careful study allows tentative conclusions as to the ancestral relations of various similar annelids and mollusks and also suggests that possible past adaptive conditions caused them to diverge. In general then, Wilson showed that cell lineage can be useful but that the embryologist must always be aware of both ancestral and adaptive influences on development.

To take the step beyond comparative embryology and delineate phylogenies would require far more research, according to Wilson. And Wilson himself was no longer interested in this work. He had by this time rejected Haeckel's recapitulation idea. In addition, his early interest in germ layers and their homologies had been replaced by an emphasis on cells, particularly on the mechanism and significance of cell division in inheritance and development. Though by 1900 Wilson's interests had shifted toward a more intense concentration on problems of heredity and nuclear changes in early development, his contribution to the emerging understanding of ontogeny-phylogeny relations was a crucial one. According to Wilson, hereditary material is adapted to past conditions and reflects the phylogenetic past. This material of inheritance passes on ancestral reminiscences in a way that may be of use to the present organism. If so, the developing characteristic is retained, while simultaneously external factors act on development from outside the organism to modify development if adaptation is advantageous. Wilson's statement that ancestral reminiscences, hereditary material, and external factors are all components of development which must be considered contained a clarification of previously confused issues that was necessary for a full understanding of the relation of ontogeny to phylogeny that Lillie articulated.

E. G. Conklin

Like Wilson, Edwin Grant Conklin worked toward his Ph.D. degree under Brooks at the Johns Hopkins University. In the summers of 1890 and 1891 he occupied the Hopkins table at the U.S. Fish Commission in Woods Hole, and he returned to Woods Hole in 1892 to study at the MBL. After some exploration of several marine materials, he had chosen for his dissertation problem the development of the gastropod *Crepidula*, a mollusk, which is closely related to the annelids.

In a paper of 1896 Conklin recognized that "embryology is but little fitted for the service into which it was so long forced, viz., the determining of phylogenies." Yet, in a view which he modified later, he maintained that embryology "holds the key to the method of evolution. . . . If ontogeny is not a true recapitulation it is, at least, a true *type* of evolution, and the study of the causes of development will go far to determine the factors of phylogeny."[32] In Conklin's view evolution is closely bound to processes of growth, assimilation, differentiation, inheritance, repetition, variation, and metabolism, and all are characteristics of individual development. He listed a series of propositions regarding development: "1. Development, and consequently evolution, is the result of the interaction of intrinsic and extrinsic factors. 2. Intrinsic causes are dependent upon protoplasmic structure. 3. Inherited characters must be predetermined in the structure of the germinal protoplasm. 4. Germinal, as compared with somatic,

32. E. G. Conklin, "Discussion of the Factors of Organic Evolution from the Embryological Standpoint," *Proc. Amer. Phil. Soc.*, *35* (1896), 78-88, quotation from p. 78.

protoplasm is relatively stable and continuous . . . [but] extrinsic causes may modify both germinal and somatic protoplasm. 5. It is extremely difficult to determine whether or not extrinsic factors have modified the structure of the germinal protoplasm. This is illustrated by some of the evidences advanced for the inherited effects of (1) diminished nutrition, (2) changes in environment, (3) use and disuse."[33] These factors should be explored through experiment, Conklin said.

In this early paper Conklin also emphasized the creative force of natural selection and supported the Darwinian idea that variations may be caused by extrinsic influences acting directly on the organism. These variations become intrinsic factors which cause differentiation in individual development, and they are then passed on through inheritance. The individual organism, as the product of extrinsically induced adaptive variations, is the product of evolution and is in itself a type of evolution. Ontogeny, as the product of evolution and the reflection of ancestral conditions, is a historical and evolutionary process, although it is not really a recapitulation of phylogeny.

This view diverged from Whitman's and Wilson's. Wilson had stressed the interplay of internal hereditary and adaptive physiological factors in development. In contrast Conklin saw development as due to intrinsic changes in the protoplasm, changes which may result from external influences acting directly on that protoplasm. This position also stands in contrast to the modern view of ontogeny, which regards ontogeny as the product of direct internal factors that are only indirectly affected and not caused by external pressures, in contradistinction to Conklin's views. Yet Conklin's views were not Haeckelian either. Like Wilson, he was concerned with the twofold basis of development, and his emphasis on the idea that all cleavage forms are not accidently and not mechanically caused but are inherited because the germinal protoplasm is highly structured underlined the fact that inherited material is often the critical factor. Although he altered his ideas later to admit that these cleavage forms may be modified by external factors, his early emphasis was important.

In an 1896 paper entitled "Cleavage and Differentiation," Conklin made a further important contribution when he introduced the distinction between determinate and indeterminate cleavage.[34] In these two cases cleavage is, respectively, either constant and differentiating or

33. Ibid., p. 78.

34. E. G. Conklin, "Cleavage and Differentiation", *Biol. Lect.*, (1896-97), pp. 17-43.

inconstant and without apparent morphological significance. Some organisms are determinate and others are not, Conklin showed. Mollusks and annelids, the phyla most studied by the men considered here and those whose cell lineages were most well known, are largely determinate. The cause of determinate cleavage must be intrinsic, argued Conklin. Differentiation could not arise from external or mechanical factors; rather protoplasmic differences which were inherited in the germinal material must be the cause. Conklin demonstrated that deterministically cleaving organisms are valuable for comparative studies of cell lineage because each developmental stage is significant, and that those studies could further be used to study phylogenetic relationships.

Conklin showed that different types of intrinsic protoplasmic differentiation lead to different cleavage patterns; for example, early cleavage may be unequal or equal, spiral or bilateral, regular or irregular. Because closely related organisms often have parallel cleavage patterns, there are cell homologies, which for Conklin are homologies in the arrangement of blastomeres and cells in the early stages. While Wilson had denied the value of using homologies to establish phylogenetic relationships, Conklin maintained in 1896 that such blastomere or early-cell homologies are useful for this purpose because:

> (1) Cleavage has a certain phylogenetic significance, and although possibly more liable to modifications than larval or adult stages and hence less trustworthy as a test of homology and of genetic relationships, it may in certain cases at least preserve ancestral conditions even after they have disappeared in end stages (annelids and molluscs). . . .
>
> (2) The early cleavages are morphologically more important than later ones. This follows from the notion of determinate cleavage, some of the earlier blastomeres being destined to form entire regions or organs of the animal, but principally from the fact that the earlier cleavages are more constant than the later ones. In all gastropods, lamellibranchs, and annelids, so far as known, the early cleavages are almost identically the same; but in later stages there are certain differences in the cleavage of various species and genera, many additional cells, for example, being found in large eggs which are not found in small ones.[35]

35. Ibid., pp. 41-42.

His own empirical studies on the early cell lineage of the gastropod *Crepidula* showed that snail to be quite similar in cleavage pattern to other gastropods and annelids during its early developmental stages. In Conklin's view the value of designating this early similarity as homologous remained despite adaptations in later stages because early cleavages preserve ancestral conditions more closely than do the later developmental stages. The early stages are "more constant, more frequently differential, and therefore morphologically more important." Elaborating, he continued:

> At first thought it may seem strange and improbable that the earlier cleavages should be more important than the later ones. It is generally, and I think truly, believed that processes of differentiation increase in extent as we approach the end stage. However, the greater differentiations of later stages are dependent upon the lesser differentiations of earlier ones, which are therefore causally the more important. Moreover, the later differentiations in general are not phenomena of individual cells, but of cell aggregates, whereas the differentiations of cleavage are primarily differentiations of individual cells. The mosaic character of cleavage is, therefore, most pronounced in early stages, whereas the cellular phenomena of differentiation become less prominent as development advances.[36]

Since Conklin saw development as caused by inherited and hence intrinsic factors, which had become modified by natural selection, he emphasized early ontogeny as a key to understanding evolutionary relationships.

A classic paper of 1897 elaborated and to some extent modified Conklin's view.[37] This paper was a valuable contribution to gastropod embryology. It was also, though secondarily, Conklin's most influential contribution to the restatement of the relation of ontogeny to phylogeny. It was widely read, having been published in Whitman's *Journal of Morphology*, and was based on careful and accurate detailed observations. In this paper Conklin carried further the distinctions between different types of cleavage which he had begun earlier. He distinguished total and partial cleavages, which result in equal or unequal products

36. Ibid., p. 43.

37. E. G. Conklin, "The Embryology of Crepidula, a Contribution to the Cell Lineage and Early Development of some Marine Gasteropods," *J. Morph., 13* (1897), 1-226.

and in equal or unequal yolk distribution. Cleavage might be regular or irregular in timing; symmetry might be radial or bilateral. And the cleavage products might have determinate or indeterminate cleavages. As a result, Conklin pointed out that Whitman's and Wilson's studies and the conclusions based on them did not hold for all organisms and could lead to confusion in the study of comparative embryology and phylogenetic relationships.[38] Only through careful comparative study of various types of organisms was Conklin able to sort out his critical distinctions of cleavage types, and only thus was he able to point out that the nondeterminately cleaving organisms would not be useful for evolutionary studies in the same way as determinately cleaving organisms would. He concentrated on a detailed cell-lineage study of *Crepidula* and compared the early cell lineage of closely and less closely related organisms.

From his comparative study Conklin concluded that there are three classes of factors which result in an organism's cleavage form. These are: (1) mechanical conditions of the ovum; (2) inherited, phylogenetic factors; and (3) prospective usefulness of a particular pattern.[39] All three classes of factors can at present be referred only to intrinsic causes, Conklin argued, and cannot be explained in terms of known mechanical conditions, such as gravity, surface tension, cohesion, and so on, as some embryologists would like to believe. True, a mechanical explanation of development should be sought, but he cautioned that biological knowledge is not yet (1897) advanced enough to succeed. Therefore, to investigate developments, the embryologist must concentrate on understanding the intrinsic factors determining cleavage patterns and the external factors influencing later development. Only then can the relative roles of mechanical, phylogenetic, and adaptive factors in development be separated, according to Conklin.

Conklin left the issue of the relation between ontogeny and phylogeny or adaptation and inheritance unanswered, though he did reject Haeckel's recapitulation. With his careful empirical study he made vital clarifications which facilitated articulation of the way in which ontogeny and phylogeny are related. His emphasis on the intrinsic structure of the protoplasm as a major factor in development was accepted, though his early ideas (which he rejected himself) about intrinsically induced internal factors were not. Perhaps his most important contribution was his clear distinction of different cleavage types and the value

38. Ibid., esp. pp. 185-192.
39. Ibid., pp. 202-203.

he placed on detailed and exact comparative observations of the earliest cleavage stages as keys to evolutionary relationships.

This point was critical because the debate about phylogenetic relationships and about whether embryos recapitulate their evolutionary past had begun to center on comparative study of the early stages. Confusion over proper interpretation of the trochophore stage, for example, reflected the inconsistencies generated by lack of understanding of those early stages. If all organisms were taken as having determinate cleavage, that is if the early stages held morphological significance for later stages, then a comparison of any one stage should be consistent with comparison of any other with regard to evolutionary relationship. But if some organisms were not determinate, as Conklin showed to be the case, then such conclusions about later and adult stages based on comparisons of early stages would not hold. What Conklin did was to separate the issue of what relation the early stages held to later stages within the same embryo from the issue of how ontogeny depends on the evolutionary past. This distinction was important, and made way for the further consideration of the latter question, with its components of ancestral reminiscence and present adaptation. In addition, the distinction facilitated a more clear-cut consideration of the first issue.

F. R. Lillie

On the advice of his teacher at the University of Toronto, Frank Rattray Lillie attended the 1892 session of the MBL. There he reportedly came into contact with Whitman very shortly after his arrival, and began accompanying Whitman on collecting trips to nearby freshwater ponds. Under Whitman's encouragement Lillie began his own study of the freshwater mussel *Unio,* which is a mollusk. He undertook a study of the cell lineage of *Unio* because of the prevailing interest in early development at the MBL. Lillie continued his study under Whitman at both Clarke University and the University of Chicago, and he received his Ph.D. in 1894 from Chicago.

Lillie's monumental study of *Unio*, which appeared in the *Journal of Morphology* in 1895, received immediate acclaim as a thorough and impressive study.[40] In that work Lillie traced the fates of each blastomere to the germ-layer stage in order to delineate *Unio* development.

40. F. R. Lillie, "The Embryology of Unionadae," *J. Morph., 10* (1895), 1-100.

He then compared this mussel with annelids and mollusks studied by Whitman, Conklin, and Wilson. The comparison led to a consideration of homologies as a criterion of ancestral similarity. Adopting a view close to Wilson's, Lillie held that cell homologies are useful but that the final test of whether cells are homologous is in their fate rather than in their origin. A complete homology will correspond with its counterpart in fate, but can also be traced back to the same germ-layer origin and to the same blastomere. Complete homologies may provide some key to phylogenetic relationships. Lillie's analysis of useful homologies demonstrates his dual concern with establishing adequate criteria of phylogenetic relationships and with making a careful and detailed study of ontogeny.

Then, temporarily separating the two issues, Lillie demonstrated a clear understanding of ontogeny in the modern sense in an 1898 paper, "Adaptation in Cleavage."[41] Though his view is similar to Wilson's in some respects, Lillie objected to Wilson's schematization in discussing ancestral reminiscence and argued that this prevented a full understanding of ancestral factors. For in overemphasizing similarities, Wilson overlooked the very differences in cleavage which are critical to development. It is "*the special features of the cleavage in each species which are, I believe, as definitely adapted to the needs of the future larva as is the latter to the actual conditions of its environment.*"[42] Lillie saw the development of *Unio* as a process guided by internal factors. After his detailed study of that organism, he concluded that for organisms with determinate cleavage the details of cleavage are "definitely adapted to the needs of the future larva." The same cannot be shown for indeterminate cleavage in which the early cleavage stages are not determinately linked with later developing differentiations. Rejecting Haeckel, Lillie held that the early cleavage stages are not primarily reminiscences carried over from ancestors; rather they are adapted to the later, larval stages.

Further, the special features of the cleavage of an organism are intimately related to the form of the ensuing larva. Thus as natural selection operates on the larval stages, it indirectly influences the early cleavage stages as well, and these latter must be adapted to the larval stages to which they give rise. For Lillie, the cleavage possibilities of the egg are limited by the cytoplasmic localizations and predeterminations inherited from the parents. So adaptations in the cleavage stages are internally

41. F. R. Lillie, "Adaptation and Cleavage," *Biol. Lect.*, 1898, pp. 43-67.
42. Ibid., p. 43.

determined, not subject to direct external pressures, but external pressures can act on the organism as a whole, creating indirect pressures for adaptation in the early stages of development as well as in the later stages. Ontogeny is therefore due to internal factors which are transmitted from the parents, but which also may be influenced by external pressures. It follows that the individual organism is a historical entity because of its heredity and that it has a historically directed course of development, though this course is modified by current adaptive dedemands at all stages of development. This is Lillie's view of ontogeny; it seems also to be essentially the modern understanding of individual development.

Having stated the nature of ontogeny, Lillie returned to the question of ontogeny-phylogeny relations in 1908 in the Introduction to his *Development of the Chick.*[43] Lillie pointed out that Haeckel's formula of recapitulation was widely accepted in 1908, but that it is not correct, that ontogeny is not the strict recapitulation of phylogeny. In fact, Lillie said, an embryo rarely resembles exactly the adult of a lower organism. Nor does an embryo exactly resemble even the embryo of a lower organism. Yet ontogenies of closely related species often appear to be quite similar because

> if we conceive that the whole life history is necessary for the definition of a species, we obtain a different basis for the recapitulation theory. The comparable units are then entire ontogenies, and these resemble one another in proportion to the nearness for relationship just as the definite structures do. The ontogeny is inherited no less than the adult characteristics, and is subject to precisely the same laws of modification and variation. Thus in nearly related species the ontogenies are very similar; in more distantly related species there is less resemblance, and in species from different classes the ontogenies are widely divergent in many respects.

The situation may be illustrated graphically, Lillie showed. Briefly, his representation is: let D be a species with ontogenetic stages A, B, C, D and let D evolve into E, F, G, H, and so on. With each step in evolution the ontogeny of the new species is closely related to that of the preceding species because in each case the adult results from modifications of a similar ovum. But the series is *not*:

43. F. R. Lillie, *The Development of the Chick* (New York: Henry Holt, 1908), Introduction, pp. 1-15.

1. ABCD
2. ABCDE
3. ABCDEF
4. ABCDEFG

Rather at each evolutionary step the early ontogenetic stages are also modified, hence the series is actually:

1. ABCD
2. A'B'C'D'E
3. A"B"C"D"E'F
4. A'"B'"C'"D'"E"F'G

Lillie's claim is not simply speculation but is based on the cell-lineage studies considered above. He had empirically observed that the earliest stages of cell division followed the second pattern rather than the first.

What this scheme does not show is the nature of the modifications of the ancestral ontogenetic stages, for "Not only is each stage of the ancestral ontogenies modified with each phylogenetic advance, but the elements of organization of the ancestral stages are also dispersed so that no ancestral stage hangs together as a unit." Thus not only the pieces but also the whole of ontogeny is modified by natural selection.

Ontogenies, according to the evidence, are not caused by phylogenies, nor do they reiterate stages identical to their phylogenetic ancestors. Ontogenies of closely related species will nonetheless be similar because ontogeny is due to the similar internal factors which are inherited by several species. Given that evolution has occurred, some relation of ontogeny and phylogeny must hold as a corollary. According to Lillie:

> But as the basis of any theory of descent is heredity, and it must be recognized that ontogenies are inherited, the resemblance between the individual history and the phylogenetic history necessarily follows. If one holds, as does the present writer, that phylogenetic variations are germinal in their character, then one must admit that every phase of development of every part has two aspects, viz.: the modern, specific, or coenogenetic, and the ancestral or palingenetic aspect. The latter aspect may be more or less completely obscured in the course of evolution, but it can never entirely vanish because it is theoriginal germ of the specific form acquired.[44]

44. Ibid., p. 6.

Ontogeny can, Lillie maintained, hold a clue to phylogeny, but phylogeny has no causal power over ontogeny. The former is a series of forms which are related by past inheritance but which have been modified continuously by natural selection operating on each species and each stage of species development with different selective pressures. Ancestral and adaptive factors in development play relatively well-defined roles in Lillie's account.

Lillie did not return to a view of development like von Baer's. He recognized that because the organism is a product of evolution, a historical entity, von Baer's analysis of development was inadequate. Ontogeny is not a progressive differentiation according to type; it is an unfolding of internal, hereditary factors -- which are reminiscent of ancestral adaptations -- in response to external pressures. Species descent must be considered in explaining individual development. Thus Lillie's view:

> Some embryologists profess to prefer the laws of v. Baer to the recapitulation theory as a formulation of the actual facts. But it is obvious that the only possible explanation of the facts is found in the theory of descent, and that therefore they must be formulated in terms of this theory. The method of formulation will depend on the conception of the nature of the factors of organic evolution.[45]

It seems clear that Lillie's understanding of ontogeny regarded the organism as a product of evolution, as von Baer's had not. Lillie's new understanding of Haeckel's biogenetic relation regarded ontogeny as a modified reflection of a phylogenetic past. Ontogeny reflects aspects of its past which are adapted to present conditions; it does not recapitulate the adult stages of that past.

In his "biogenetic law" Haeckel had claimed that ontogeny recapitulates phylogeny. Lillie showed that ontogeny does not recapitulate phylogeny, but that it does reflect those aspects of phylogeny which are adapted to the present needs of the organism. It is, I believe, Lillie's view which Balinsky adopts when he says in his embryology textbook that the modern "biogenetic law" is a synthesis of von Baer's and Haeckel's views. As Balinsky states the modern law:

> Briefly, the features of ancient origin develop early in ontogeny; features of newer origin develop late. Hence the ontogenetic develop-

45. Ibid.

> ment presents the various features of the animal's organization in the same sequence as they evolved during the phylogenetic development. Ontogeny is a recapitulation of phylogeny. The repetition is obviously not a complete one, and the biogenetic law states that "Ontogeny is a shortened and modified recapitulation of phylogeny." The shortening of the process is evident not only from the fact that what had once taken thousands of millions of years (phylogeny) is now performed in a matter of days and weeks (ontogeny), but also from the fact that many stages passed through in the original phylogenetic development may be omitted in ontogeny. The modifications arise mainly because the embryo at any given time is a living system which has to be in harmony with its surroundings if it is to stay alive. The embryo must be adapted to its surroundings, and these adaptations often necessitate the modification of inherited features of organization.[46]

It is important to separate what Lillie's work did from what it did not do. It did clarify on the general level the sense in which ontogeny is related to phylogeny. It did emphasize that adaptation is critical but that ancestral contributions to embryological development also play an important role. It did not delineate exactly the nature of development in terms of ancestral, inherited and adaptive factors; it did not explain the details of development, and in fact no one has yet fully done so. Lillie's work, in conjunction with that of the others, did separate a number of previously confused issues into relatively well-defined questions on which it was possible to carry out productive research.

CONCLUSION

The understanding of ontogeny as a product of heredity and adaptation to present conditions which reflects but does not recapitulate phylogeny was achieved by six American embryologists who worked on comparative studies at Woods Hole. Whitman provided the example for carrying out careful and detailed cell-lineage studies, which followed the pattern of cell division in the earliest developmental stages. Thus Whitman shifted from Haeckel's emphasis on the germ layers back to the cellular origins of those germ layers. He illustrated the value which these early cell-lineage studies may have for tracing phylogenetic relationships. Wilson carried Whitman's work further and added the

46. Balinsky, *Introduction to Embryology*, p. 9.

critical clarification of the relative roles played by hereditary factors, or ancestral reminiscences, and environmental adaptive factors in ontogeny. Conklin distinguished different patterns of cell lineage and showed that early subtle differences in determinately or indeterminately cleaving organisms give different information that is important for understanding ontogeny and for tracing phylogeny. Mead and Treadwell provided further cell-lineage data. This empirical and theoretical work culminated in Lillie's expression of the modern ontogeny-phylogeny relation, which was based on the strong edifice of comparative embryology made possible by the individuals discussed.

This cell-lineage work provided a transition away from Haeckel's naive causal biogenetic law and his preoccupation with tracing phylogenetic trees. Lillie, building on the work of Whitman, Wilson, Conklin, Treadwell, and Mead, recognized that Haeckel's biogenetic law and recapitulation idea were inadequate, and articulated a modern understanding of the relation. Incorporating the concern of von Baer and His for the problem of individual development in itself, these American embryologists moved beyond both to a new understanding of the genetic relation of ontogenies. Though not a central focus of the cell-lineage work and therefore easily overlooked, the intellectual contribution made by the six men discussed above was important. By clarifying the relations of ontogeny and phylogeny they also cleared the ground for independent investigations of development and of systematics.

Whether their views on the biogenetic relation influenced many others directly I have not yet discovered. Certainly, their own work profited by the clarification of the ontogeny-phylogeny relation and from the close analysis of ontogeny as the product of ancestral and adaptive factors. Probably their excellent cell-lineage and later studies also served as guides for similar studies or for different approaches to similar questions. I do not want to claim that the work of Lillie and the others also resolved the debate over whether or how recapitulation occurred. That it did not do so is suggested by the existence of Gavin De Beer's book on recapitulation and the germ-layer theory published in 1930 and revised in 1951 and 1958.[47] Yet the work of the six Americans is significant as a short chapter in a longer story about the history of the recapitulation idea because whether it was widely influential or not, it is clear that by 1908 Lillie had achieved a modern

47. Gavin De Beer, *Embryos and Ancestors* (Oxford: Oxford University Press, Clarendon Press, 1958), revised from *Embryology and Evolution.*

understanding of the general relation of ontogeny to the evolutionary past.

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