C.H. WADDINGTON AND MODERN EVOLUTIONARY THEORY

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ABSTRACT: Waddington's evolutionary orientation in the 1940s and 1950s was at odds with that of most leading American evolutionists. Waddington stressed the integrative capacity of developmental process, whereas integration of genetic system figured much more importantly in the prevailing evolutionary theory. In Waddington's view, his theory of genetic assimilation founded a new "post-neo-Darwinian" paradigm which, unlike older paradigms, did not invoke processes of "random search" in the explanation of evolutionary adaptation. Yet "random search" processes are always anterior and prerequisite to the assimilative processes upon which Waddington focused his attention. Genetic assimilation, therefore, is not a revolutionary theory; rather, it is an important articulation of "neo-Darwinian" evolutionary theory. The range of Waddington's evolutionary thought is unfortunately limited. With the exception of the problem of adaptation, he does not, as a general rule, treat of concrete, specific evolutionary problems in depth. When he does discuss specific evolutionary issues, his treatment is generally brief and highly theoretical, and hardly suitable to the task of directing positive research. Again, Waddington's claim of paradigm reformulation appears insupportable.

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Waddington's Evolutionary Thought: Background

The rediscovery of Mendelian genetics in 1900 set the stage for a radical transformation of Darwinian theory. In the course of the first 30 to 35 years of this century, population genetics came to play an increasingly important role in evolutionary theory; for much of the second quarter of the century, the mathematical models of Fisher, Haldane and Wright figured centrally in important circles of evolutionary thought. In the years of 1930 to 1960, however, the view of the evolutionary process associated with the Fisher-Haldane-Wright "classical population genetics" was subjected to severe and general criticism. C.H. Waddington was, without a doubt, one of the most vehement and persistent critics of classical population genetics, which he rather idiosyncratically preferred to term the "neo-Darwinian paradigm."

Waddington's description of the "neo-Darwinian" model of evolutionary process can be summarized in three points: 1) genes are isolated functional unities whose selective value remains invariant in different genetic milieus; 2) genetic variation is provided by a process of gene mutation-recombination that is totally random, i.e. wholly independent of selective (or other directed) processes; 3) adaptation is the byproduct of a process of natural selection acting upon genes (again, this selective process is wholly independent of the genes upon which it acts). In Waddington's own words:

> ... the evolutionary system ... has often been envisaged as consisting of no more than a set of genotypes which are influenced, on the one hand, by a completely independent and random process of mutation and, on the other, by processes of natural selection which again are in no way determined by

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> the nature of the genotypes submitted to them.[1]

Waddington could not abide this "random search" model of the evolutionary process. He was, of course, a professional developmental biologist, and objected most vigorously to the "neo-Darwinian" trivilization of the all-important difference between genotype and phenotype. Waddington's own conception of the evolutionary process was premised upon close attention to epigenetic phenomena, most particularly the following points:

1) phenotypes are the manifestations of complex and coordinated systems under genotypic control.

2) the environment may be very directly involved in epigenesis.

3) development generally tends toward relatively definite end states (e.g. a discrete organ), and there is a canalization of development pathways which buffers the developmental system from disruption by environmental and genetic abnormalities.

These epigenetic concepts immediately contradict the premises of the "neo-Darwinian paradigm," especially its assumption that genes act as independent units of function and possess fixed selective value. Thinking of the phenotype in developmental terms (point 1), as a set of epigenetic processes rather than simply the inevitable morphological and physiological result of those processes, is incompatible with "bean bag," or classical population genetics, for the complexity and coordination of developmental processes imply that the genetic system which underlies these processes is interactive, and to some extent, integrated. This, in turn, leads directly to the realization that it generally makes very little sense to speak of the selective value of an individual gene, for the selective value of any particular gene must be contingent upon how it functions in combination with the rest of the genotype--it depends on the genetic milieu. Relatedly, canalization provides that a genetic change may well not lead to phenotypic change, and this again belies the artificiality of labeling genes with fixed selective coefficients. Lastly, point 2 reveals a sometimes insufficiently appreciated cybernetic connection between selective pressures and genotypes, and thus contradicts the third principle of "neo-Darwinism" cited above.

Thus, the most basic epigenetic principles cannot be accommodated within the framework of classical population genetics, and epigenetics undoubtedly played an important part in the abandonment of classical population genetics. The first point stressed above is of particular importance in this connection. Indeed, the repudiation of classical population genetics can hardly be disassociated from the rise of genetic integrationist theories. For example, the penultimate section of Ernst Mayr's 1955 CSH article is entitled:

> THE NEW POPULATION GENETICS
>
> The title of today's discussion, the integration of genotypes, is indicative of the trend of development in this field. Classical population genetics dealt with absolute values, genes were either contributing to fitness or were deleterious. Expressed in mathematics it described the essential properties of populations in terms of frequencies of genes. The current Symposium has focused attention on a

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[1] C.H. Waddington, <u>The Evolution of an Evolutionist</u> (Ithaca: Cornell University Press, 1975), p. 58. It should be noted that very few, if any, of the leading evolutionists of this century actually held such a simplified conception of the evolutionary process.

> development which has been gathering momentum for some years. It is, so to speak, a theory of relativity in the field of population genetics. A gene is no longer considered as having a fixed, absolute selective value. Rather its contribution to fitness is relative and may change. It depends on the nature of the genotype of which it is a component....[2]

The tie with epigenetics surfaces later in the article:

> According to classical genetics a gene produces a chemical (a gene product), which in turn affects one or several characters, which in turn determine the visibility or the selective value of the bearer of this gene. Not only the chemical nature of the gene product, but also the period in the developmental process when it is produced, and the average amount produced may be specific properties of genes. Nevertheless we are no longer convinced that this determines automatically a fixed viability. After all, a gene product does not shape an organ directly, rather it enters into a developmental process. The evolutionary fitness of the final phenotype depends on the suitability of this gene product to contribute to the development of a superior phenotype in collaboration with all the other gene products and in the respective environment in which the zygote develops.[3]

Yet caution is in order here. Despite the causal link connecting genetic and developmental phenomena, a sophisticatedly epigenetic evolutionary perspective is not compatible with an unreserved endorsement of genetic integrationist theory. It is therefore not surprising that Waddington was by no means in complete accord with the theories of genetic integration which gained such prominence in the 1940s and 1950s in America. His evolutionary orientation remained, to a significant degree, genuinely different from that of the American mainstream. The remainder of this section attempts to elucidate the broad outline of Waddington's evolutionary thought within the context of a theoretical confrontation with genetic integrationist ideas.

The concept of genetic integration was originally applied on the level of the genotype. This is typified by Dobzhansky's "balance theory," a theory of co-adaptation (balance and cooperation) among the genes of the individual organism. In Dobzhansky's view, the history of evolution entailed the evolution of increasingly complex and coordinated developmental systems, and this in turn implied increasing co-adaptation of the genotypes that controlled these developmental systems:

> Progressive evolution has, on the whole, led to a greater and greater complexity of the developmental processes, and accordingly to more and more interdependence and integration of the gene-induced reactions.[4]

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2. Mayr, E., "Integration of Genotypes: Synthesis," Cold Spring Harbor Symposium on Quantitative Biology 24 (1959): pp. 332-33.

3. Mayr, E., CSH Symposium 24 (1959): p. 327.

4. Dobzhansky, T., "The Evolution of Genes and Genes in Evolution," CSH Symposium 24 (1959): p. 26 and p. 23.

The investigation of the genetics of natural populations was also of great importance in the shift from classical to the new population genetics. Thus Dobzhansky (CSH 1955) states: "Evolution involves far-reaching reconstruction of integrated gene systems. Evidence of this comes, before all else, from genetic analyses of differences between related species, and also between

Dobzhansky tended to stress the controlling role of the genetic system, and viewed the co-adapted genotype as the fundamental source of developmental coordination, and integrative capacity in general. His view in this connection was more or less typical. Waddington, however, did not feel that the complex coordination of developmental processes required a corresponding degree of genetic integration. Whereas for Dobzhansky "more and more interdependence and integration of the gene induced reactions" clearly implied more and more integration of the underlying genotypes, Waddington did not feel the strict necessity of the equation. In fact, Waddington believed that the developmental processes themselves, rather than the underlying genetic system, served as the most important level of coordination. In an article entitled, "The Integration of Gene-controlled <u>Processes</u> and Its Bearing on Evolution" (emphasis mine), Waddington states,

> The first point to be noticed about the living things which confront us when we turn our attention to the processes of evolution or to the phenomena of development is the outstanding fact which we acknowledge when we refer to them as [organisms]--the fact, that is to say, that they are integrated systems, each of whose parts is related by an intricate nexus of reaction and interaction with every other part. This integration or organisation forces itself on our attention in the first place as a characteristic of the entire functioning animal. It is an organisation of physiological processes, and since these processes must themselves be ultimately controlled by genes, it follows that what we first notice is an integration of gene-controlled processes. This is the prior phenomenon with which we have to deal. Now it is of course true that this integration has been built up during the course of evolution, and it is possible that, to a greater or lesser extent, evolution of the genetic determinants themselves, for instance by the formation of co-adapted complexes held together by inversions or close linkage. But it should be emphasized that the phenomenon of integration which challenges us for an explanation is integration at the level of the organism and its functional parts; integration at the level of the gene is a secondary affair, to be either postulated on theoretical grounds or revealed by more or less subtle experimentation. There is no a priori reason why there should not be a considerably greater degree of integration of the gene-controlled processes than there is of the genes

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subspecies or races." Yet, despite this strong statement, it is questionable that mere observation of the polygenic differences pervading natural populations could, of itself, lead to a pronounced emphasis on genetic integration. Recognition of the ubiquity of gene interaction does not necessarily demand the emphasis on coadaptation so prominent in evolutionary theory in the 1950s. In addition to field population genetics, experimental population genetics and plant and animal breeding work were undoubtedly of primary importance to the rise of the "New Population Genetics," and some workers (e.g. Wright) in these experimental disciplines did interpret their results in an epigenetic perspective. A thorough study of all the developments which led evolutionists to reformulate evolutionary theory upon the "New Population Genetics" and repudiate to no small degree, "classical population genetics," cannot be offered here.

> themselves: and we shall see that there is good reason to believe that this is in fact the case.[5]

Waddington then goes on to discuss cellular reactions and attempts to use differential equations to show that "if the synthetic processes (cellular reactions) interact with one another in the way we have discussed," a set of stable end-states, or equilibrial positions will result; he states,

> Such a system then, would exhibit the two major characteristics of developmental canalisation; it would tend towards one or other of a finite number of distinct end-states, and the attainment of a particular end state would be relatively independent of minor variations in the early conditions.[6]

For Waddington, the "cybernetic," autoregulatory qualities of development derive primarily from integration _above_ the level of the underlying genetic system.

Given Waddington's emphasis on developmental integration, it was only natural that he should doubt the plausibility of many of the arguments that underlay genetic co-adaptation theory. Waddington was not convinced of the existence of genetic mechanisms which would permit an extremely high degree of genetic integration to be maintained in a population, and felt that those genetic mechanisms which had been suggested were inadequate in this regard. Thus, in the following passages, he rejects linkage and heterozygosity as adequate explanations for the integration of gene-controlled processes:

> Quantitative characters often do not behave in inheritance as though they are controlled by independent additive genes, but rather as though they are "integrated" or "coordinated" in some way. One attempt to cope with the situation has been made by Mather...he postulated some purely genetical complications to explain the appearance of integration, suggesting that there is a special category of genes concerned with such characters, that they are linked together into balanced complexes. This theory has, however, not been regarded as adequate in general, although it may apply in particular cases..._the problem is not solely genetical_..._the integration is largely a property of the developmental system producing the character_.[7]

And again,

> ...the point which I wish to make is that the developmental canalisation cannot be fully accounted for in terms of the types of integration of the genetic elements which have so far been suggested. Thus a canalised process may be affected by genes in many different chromosomes, and the organisation of the process cannot arise to any large extent from genetic linkage. Similarly, developmental buffering cannot be attributed solely to obligatory heterozygosity, both because it must certainly involve inter-locus interactions, and because it occurs in connection with genes which cannot be heterozygous (e.g. sex-linked ones in the heterogametic sex). Both linkage and heterozygosity may, of course, play a part in the buffering of the action of a genotype which has been subjected

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[5] C.H. Waddington, "The Integration of Gene-controlled Processes and Its Bearing on Evolution," _Caryologia_, Supplement to Volume VI (1954): pp. 232-233.

[6] Ibid., p. 236.

[7] _Strategy of Genes_.

> to natural selection but they are to be regarded as secondary improvements on a system of canalisation whose basic mechanism is of another kind.[8]

Waddington's particular orientation is also reflected in his de-emphasis of the importance of physiological genetics for evolutionary theory. It is significant that he entitled his most extensive work on evolutionary issues The Strategy of Genes. In the introductory chapter, Waddington states:

> [Developmental genetics and the study of the genetic constitution of natural populations] are mainly concerned, however, with what I should venture to call tactical questions. They aim at elucidating the way in which individual genes operate during development, or the nature of the genetic differences between very nearly related populations which may or may not be engaged in any major evolutionary advance. I wish to discuss the strategic question: how does development produce entities which have Form, in the sense of integration or wholeness, how does evolution bring into being organisms which have Ends in the sense of goal seeking or directiveness?...
>
> It may even be that the answers to the most basic tactical questions are not merely inessential, but are actually more or less irrelevant, to the strategic problems ... if we decide that selection operating on the genetic system of population can bring about gradual alterations of the metric characteristics of its individuals, it is more or less irrelevant to the evolutionary consequences of these changes whether they depend on a special class of gene-loci such as the heterochromatic polygenes invoked by Mather, or on a special type of allele, such as the iso-alleles of Stern and others, or whether there is nothing very special about the genes at all, except that their effects are rather small. Again, the tactical problems, immensely interesting as they are, and fundamentally important in their own context are largely irrelevant to the strategic questions.[9]

Waddington's drift here is consistent with his opinion that integrative capacities lay primarily within the developmental, rather than the genetic, system. Given this position, detailed understanding of the way to which genes control the preliminary biochemical reactions in ontogeny is of no great use in solving evolutionary problems. On the other hand, if genetic system itself is supposed to be the primary level of integration, detailed investigations of the manner in which genetic integration is achieved, maintained, and manifested in the first stages of development are of great evolutionary consequence. Thus, Mayr's article, "The Integration of Genotypes: Syntheses," he states,

> Such phenomena as balanced polymorphism, heterosis, and epitasis are definitely in the zone of overlap of [developmental and population genetics]. A number of different treatments of these phenomena are possible and were attempted by one or the other contributor to this Symposium. Neither the purely mathematical-genetic form of treatment (additive, etc.,

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8. Ibid.
9. Ibid., p. 9, 10.

> contribution to the fitness of the genotype) nor the purely evolutionary treatment (selective value, adaptedness) has been a full success. This is not surprising since both lead to interpretations that are based on an oversimplified analysis of second order phenomena. A full understanding of these phenomena cannot be expected unless they are interpreted in terms of gene action, that is in terms of physiological genetics.[10]

Lerner (1955) strikes a similar chord,

> I would like to note the impression that much of our work manifests the need to bring into camp physiological and developmental geneticists working at all levels of individual differences from isolated allelic substitution of the genotype as a whole. It may be illegitimate or irrelevant to ask <u>why</u> of pop genetics; the what can be answered by observation and statistical analysis; but the how will find its reply in ecological, physiological, embryological, biochemical...studies of gene interaction and balance. Population genetics may not engulf all of genetics, but it is indeed ready to exploit much of the information and many of the techniques of the other branches.[11]

as does Stebbins (1959),

> The conclusion which we can reach from the present symposium regarding this first unsolved problem is that our efforts to understand the action of natural selection in higher organisms will be increasingly thwarted by our ignorance of developmental genetics, on which the "why" of selective advantage largely depends.[12]

In the late 1940s, many evolutionary theorists tended to concentrate upon developing theories of <u>genotypic</u> co-adaptation; in the 1950s, many evolutionists shifted their focus to theories of genetic integration on the level of the Mendelian population. While it is not easy, conceptually or mechanistically, to consider the integration of the genotype and integration of the <u>gene pool</u> as separate phenomena, it is indubitable that an increased emphasis on the population rather than the individual had subtly altered the context. in which evolutionary problems were considered by the mid-1950s. Ample evidence for the reality of this shift may be found in the 1955 CSH symposium. For example, Lerner, in his concluding survey, lists "the significant landmarks of population genetics in the 30 or 40 years since its genesis"; the last two "landmarks" are:

> (5) The origin and expansion of the concepts of balanced and co-adapted genotypes together with the efforts to determine their genetic bases; and (6) The deduction of the existence of an integrated structure in Mendelian populations and the consequences arising therefrom.

Lerner goes on:

> It is the last point mentioned which I would consider to provide us with the most excitement at the moment, and which is the essence of the current instar of evolutionary thought... because of it we are moving towards a more sophisticated view

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10. E. Mayr, <u>CSH</u> 20, p. 327.
11. I.M. Lerner, <u>CSH</u> 20, p. 337.
12. G.L. Stebbins, <u>CSH</u> 24, p. 307.

> of evolutionary processes. (Recognition of the existence of supra-individual entities leads us to question some of our cherished assumptions about nature and about breeding improvement.)
>
> Although not all of the papers presented reflected this new stage of population genetics, nor, do probably all the participants share my enthusiasm for it, a major part of our debates was colored by awareness of it. Indeed, I would say that most of the work discussed here, about which it is possible to make generalisations, contributes perhaps against the desires of some of the authors, to the elaborations of the concept of population properties as contrasted with those individuals.[13]

Many of Waddington's evolutionary ideas contested the theoretical premises of genotypic co-adaptation; this conflict is only exacerbated when genetic integration of Mendelian populations comes under question. Waddington's developmental orientation was intrinsically bound to an emphasis on individual (rather than population) level integrative capacities, for epigenetic development is solely a phenomenon of the individual. Furthermore, in the systematic relations of the evolutionary process, the integrative capacity present at the level of the individual reduces the potential for integration of the <u>population</u> gene pool. The production and maintenance of a high level of population level genetic integration must depend upon a fairly strict and durable selective regime, yet many developmental phenomena tend to relax the stringency of selection. The self-regulating properties of developmental reactions render superbly integrated genotypes (and gene pools) unnecessary; strong developmental buffering (canalisation) may neutralize the negative effect of potentially deleterious genes and inharmonious gene combinations, and thus shield such genes (and gene groups) from selection. Genetic homeostasis--the persistence of particular genes and/or gene groups in a population --is associated with genetic integration; Waddington states:

> ..the evolution of a canalisation is, in some ways, antagonistic to genetic homeostasis. The more narrowly canalised is the development of a character, the less will changes in gene frequency come to phenotypic expression, and the less will be the tendency to genetic homeostasis.[14]

In general, then, the capacity of natural selection to fine-tune and integrate a gene pool is diminished by the auto-regulatory coordination of developmental processes. Thus, a criticism of population integration theory can be built upon two premises: (1) selection acts primarily on the level of the individual; population level genetic integration must therefore occur as a by-produce of selection acting on the level of the individual, but (2) individual level selection produces developmental integrative capacity that hinders, rather than fosters, the evolution of integrative capacity at the level of the population.

Few evolutionists in the 1950s perceived this objection clearly; the rather simple premises of the criticism were not well assimilated into the evolutionary mainstream in the 1950s. Unfortunately, the population emphasis in the 1950s was so pronounced that certain evolutionists did not recognize the first premise. For example, Dobzhansky, in his renowned third edition of <u>Genetics and the Origin of Species</u> (1951), often states bluntly that the

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[13] I.M. Lerner, <u>CSH</u> 20, p. 335.

[14] Waddington, <u>Strategy of Genes</u>, p. 42.

Mendelian population is the unit of selection. In the following quotation from the 1959 CSH Symposium Dobzhansky appears totally oblivious to the problem of effective level of selection:

> The challenges of the environment are...met by [higher organisms] in two ways. On the individual level, the adaptedness lies in a homeostatic buffering of the developmental pattern. On the population level, a great array of genotypes is built to exploit the different spatial and temporal facies of the environment.[15]

This passage illustrates quite clearly that Dobzhansky did not feel the need to establish explicit connections between the genetical implications of developmental homeostasis for the individual, on the one hand, and the population, on the other. Rather, Dobzhansky implies that the population responds to selective pressures in a way distinct from the response of its constituent individuals, giving no indication that the genetical implications of developmental homeostasis may be of great consequence to the constitution of the gene pool.

Similarly, premise 2 was often poorly understood. Many evolutionists in the 1950s held serious misconceptions about evolution-related epigenetic issues. For example, in 1953, Simpson devoted a whole article to the Baldwin effect ("organic selection") in which he revealed virtual total ignorance of Waddington's much more sophisticated ideas on the issue of the role of environment in the evolution of adaptations. Dobzhansky also evidenced serious misunderstandings concerning developmental canalisation and its implications.

> Waddington's 'canalisation': is evidently a part of the general physiological phenomenon of homeostasis as defined by Cannon (1932). Homeostatic maintenance of the 'steady state' of the organism in the face of changing environments is possible only thanks to a remarkable plasticity of the physiological machinery. For example, the ionic concentration of the blood in mammals remains constant because the kidneys are working differently when too much or too little salt is ingested. The 'steady state' which is maintained is that which permits the body to remain alive and to continue its development along one of the phylogenetically established adaptive paths. <u>Functional homeostasis</u>, with its marvelous reversible reactions, which are so important in the maintenance of health and well-being, thus results in <u>developmental homeostasis</u>.[16]

Waddington correctly points out that this is all wrong.

> ...canalisation is, in some ways, antagonistic both to genetic homeostasis and to physiological homeostasis..a high capacity for physiological homeostasis implies that when the environment is altered development will be modified in such a way that the organs can carry out their physiological functions with normal efficiency in the new circumstances, and this may necessitate a departure from canalisation.[17]

Dobzhansky and Simpson could hardly think intelligently in the matter of canalisation, selection level, and evolution given such poor understanding of developmental buffering.

I. M. Lerner understood the selection level problem quite clearly:

> It seems obvious that properties of populations, as much as

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[15] Dobzhansky, <u>CSH</u> 24, p. 24.
[16] Dobzhansky, <u>CSH</u> 20, p. 7.
[17] Waddington, <u>Strategy of Genes</u>, p. 42.

> properties of individuals, have evolved under the action of natural selection. At the same time it is not immediately clear as to how natural selection operating on the individual level could lead to the development of integrating factors at the level of populations. Many students of evolution (e.g. Fisher, 1932, Simpson, 1941) have stressed the fact that natural selection cannot be concerned with properties of units higher than the individual....The evolution of the integrative characteristics of Mendelian populations must have occurred under this view as a by-product of individual selection.[18]

Lerner, alone among evolutionists, tackled this reticulative problem head on, and attempted to "construct a genetic model on the basis of which the more complex integrative properties of Mendelian populations can emerge from evolutionary forces operating on individual genotypes."[19] Yet, Lerner also evidenced an unsatisfactory understanding of evolution related developmental issues--his model was built upon Waddington's concept of canalization! Lerner's thesis that heterozygosity per se acts as a homeostatic device on both the individual and population level was, by 1959, widely held to be largely invalid. Waddington himself, of course, held it to be theoretically implausible.

Problems of selection and epigenetic phenomena are also confused in Schmalhausen's influential Factors of Evolution. In this text, Schmalhausen stresses the role of "stabilizing selection" in evolution. Waddington clarifies that this term covers two very different selective processes. The first, which Waddington calls "normalising selection" is the process by which "selection may act in a stabilizing manner to preserve the original phenotypic character by eliminating new deleterious mutations." Waddington describes this type of selection as a mechanism promoting genetic homeostasis, à la Lerner.

> ...a population inhabiting a uniform environment exhibits a phenomenon which has been called 'genetic homeostasis' (Lerner, 1954). The frequency with which any particular gene is present in the population settles down to an equilibrium which is determined by the pressures of selection, mutation, migration, etc. If some slight change from the equilibrium position is brought about...then these pressures will bring the frequency back to the equilibrium, the selection pressure being usually the most effective magnet in this return.[20]

Because it enhances genetic homeostasis, normalising selection is clearly eminently suited to foster coadaptation of gene pools. This is not the case with the other mode of "stabilising selection," which Waddington terms "canalising selection" and describes as follows:

> Phenotypic constancy and uniformity of a population could be ensured by selection in favor of genotypes which control developmental systems which are highly canalised and therefore not very responsive either

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[18] I.M. Lerner, Genetic Homeostasis (New York: John Wiley and Sons, 1954): p. 4.

[19] Certain other evolutionists (e.g. Mayr) did recognize this problem more or less clearly, but Lerner apparently felt its importance most urgently. Whereas Genetic Homeostasis is a full length book devoted to this problem, no other evolutionist proferred a comprehensive solution in print.

[20] Waddington, Strategy of Genes, p. 72.

> to abnormalities in the environment or to new gene mutations of a minor character.[21]

Clearly, it is canalising selection which poses problems for the concept of the integrated gene pool. Waddington is correct in claiming that, while Schmalhausen describes both types of selection, he fails to distinguish them explicitly. For example, in one important passage in an introduction to a section, Schmalhausen describes the two forms of selection, but terms them both stabilising selection, and his discussion of one blurs ambiguously into his discussion of the other. He does not, in any one place, clearly expound the evolutionary implications of one of these types of selection, and then discuss the very different evolutionary implications of the other.

Waddington's general conception of the system of evolution, in its emphasis on the integrative capacity of developmental processes rather than genetic systems, differed significantly from that of many important evolutionists. Furthermore, it is apparent that Waddington had a clearer conception of the problems relating to selection level, canalisation and developmental coordination and evolution than most evolutionists. The question remains: to what extent did Waddington, building upon his epigenetic-evolutionary premises, formulate a comprehensive and coherent new view of evolutionary process--i.e. succeed in articulating a "post-neo-Darwinian paradigm"? An answer to this question demands moving from broad evolutionary outline to an analysis of Waddington's treatment of specific fundamental evolutionary problems.

A CRITICAL ANALYSIS OF WADDINGTON'S EVOLUTIONARY THOUGHT:
PART I: THE PROBLEM OF ADAPTATION

In his career as evolutionist, Waddington focused most of his energies upon that issue which he considered least explicable within the framework of the prevailing neo-Darwinian theory: the problem of adaptation.

Waddington did not believe that a mechanism of random mutation and non-teleological selection could produce the remarkable adaptations so familiar in the natural world. In an article entitled "Does Evolution Depend on Random Search" Waddington quotes and tacitly concurs with the following statement:

> According to molecular biology, we have a space of objects (genotypes) endowed with nothing more than a typographic topology. These objects correspond (by individual development) with the members of a second space having another topology (that of concrete physico-chemical systems in the real world). Neo-Darwinism asserts that it is conceivable without anything further, that selection based upon the structure of the second space brings a statistically adapted drift (effecting adaptation), when random changes are performed in the first space in accordance with its own structure. We believe that this is not conceivable.[22]

Waddington felt that a satisfactory solution to the problem of adaptation could only be achieved within the framework of an evolutionary theory premised upon a sophisticated understanding of epigenetic principles. The three epigenetic principles previously outlined are all incorporated in his "solution" to the problem of adaptation, the theory of genetic assimilation.

Waddington (1975) describes the process of genetic assimilation as follows:

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[21] Ibid., p. 72.

[22] Waddington (1975), p. 184.

> The process of genetic assimilation is one by which a phenotypic character, which initially is produced only in response to some environmental influence, becomes, through a process of selection, taken over by the genotype, so that it is formed even in the absence of the environmental influence which had at first been necessary.[23]

The mechanism of genetic assimilation can perhaps best be described by comparing it with that of "organic selection," a concept first discussed by James Mark Baldwin and C. Lloyd Morgan around the turn of the century. The processes of genetic assimilation and organic selection can be most easily conceptualized with the aid of Waddington's diagrammatic representation of the "epigenetic landscape" (Fig. 1).

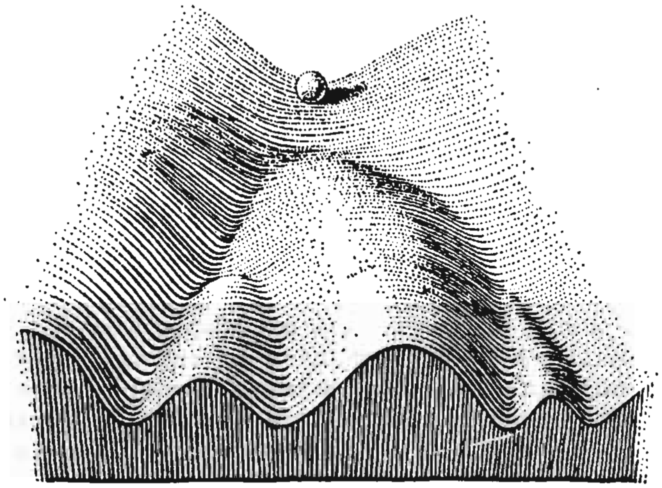

Figure 1. The epigenetic landscape.
(All figures reprinted from C. H. Waddington, The Evolution of an Evolutionist. Copyright © C.H. Waddington 1975. Used by permission of publisher, Cornell University Press.

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The typography of the landscape is determined by the genotype. Each point on the landscape represents a different phenotypic state, and the course of development is represented by the ball rolling down the landscape. It is clear that development will tend to proceed along certain pathways--the valleys of the landscape--toward discrete endpoints. While genetic or environmental abnormalities may push the ball away from the valley floor up a hillside, if the ball is not pushed over a hill, it will tend to return to the valley floor in the normal course of developmental buffering, or to use Waddington's own terminology, developmental "canalisation."

A comparison of the processes of genetic assimilation and organic selection

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[23] Waddington (1975), p. 59.

in reference to a trait involving developmental thresholds[24] is illustrated in Figure 2.

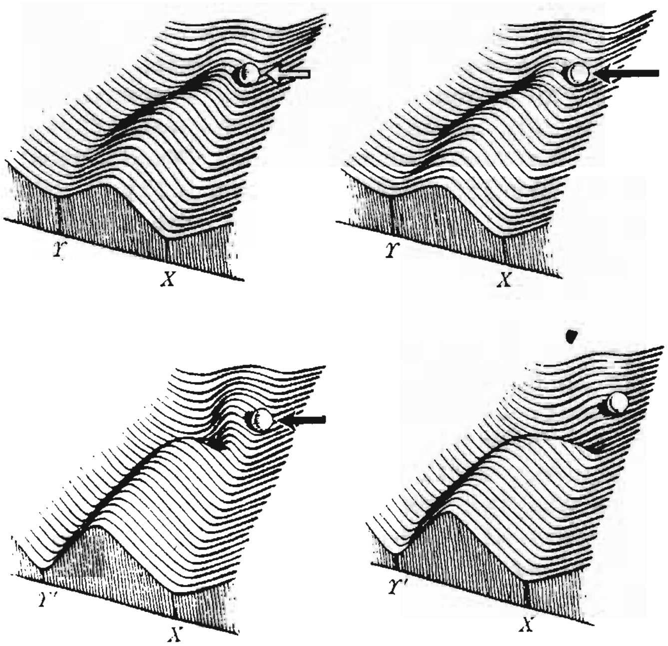

Figure 2. Modification of the epigenetic landscape by selection. The upper left drawing shows the situation in the unselected foundation stock; a developmental modification Y will occur only if an environmental stress (white arrow) forces the developing system to cross a threshold or col. The upper right figure shows the Baldwin-Lloyd Morgan hypotheses--that a new gene mutation (black arrow) appears which substitutes for the environmental stress, everything else remaining unaltered. The two lower figures show stages in the selection of genotypes in which the threshold is lowered (requiring only a 'small' gene mutation or, eventually, a single specifiable mutation) and the course of the developmental modification is made more definite and directed to the optimal end-result, Y^1.

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24. Phenotypic traits may be classified into two types for purposes of simplicity. First, there are those traits which are generally manifested in an all or none fashion (e.g. crossveinless wings in Drosophila). The development of these traits presumably involves thresholds: i.e. if a certain level of biochemical activity is attained, the trait will be manifested in normal form, while if biochemical activity remains below that threshold, the trait is not manifested at all. The second type of trait is not manifested in an all or none fashion; a gradation of phenotypic expression is possible (e.g. ostrich callosities). The development of this type of trait presumably does not involve threshold phenomena. The principles of the genetic assimilation process are identical for both types of traits; however, threshold traits lend themselves more easily to diagrammatic representation.

The comparison is more clearly illustrated in diagrammatic form for threshold traits, but the principles remain the same for non-threshold traits.

As Waddington correctly points out, organic selection does not depend upon the fact that the genotype controls an organism's capacities to react adaptively to external exigencies. If phenotype A is advantageous in new environment E, "genetic assimilation" of phenotype A must wait upon the chance occurrence of a discrete mutational or recombinational event mA, which produces A. The capacity of the organism to develop A somatically within environment E is not important in this mechanism, for the selective pressures associated with E play no role in "setting the stage" (Waddington) for adaptive mutational change; they do not increase the probability of mA.

Waddington emphasizes that the complexity of the genetic control of development makes it improbable that a single mutational event could produce anything but the simplest physiological or morphological adaptation, and he therefore discards organic selection as a general mechanism of genetic adaptation. On a more fundamental level, he points out that regardless of whether or not organic selection occurs in nature, the concept itself contains nothing whatsoever novel for evolutionary theory. The "theory" amounts to the observation that the ability of the organism to develop somatic adaptation may enable them to remain in a new environment until favorable mutations occur and dress them out in a genotype appropriate for their new surroundings.

In contrast, the process of genetic assimilation is premised upon important and novel sophistications of the older neo-Darwinian explanations of adaptation, which were traditionally couched wholly in terms of the statistics of random mutation and selective coefficients. The remodeling of the epigenetic landscape which transpires in the course of genetic assimilation does, of course, occur through mutations which are random with respect to the environment. Yet, in attempting to understand the evolution of adaptations, it is crucial to recognize, as Waddington did, that a rather rigid genetic determination of a particular phenotype may be built up in many small genetic steps, each slightly favorable mutation (at least originally) requiring assistance of an environmental stimulus to allow expression of the favorable phenotype, and thus manifestation of the selective advantage of that mutation. Thus, while individual mutational/recombinational events are completely random throughout the process of genetic assimilation, there is a directed reconstruction of the (population) genetic structure and epigenetic landscape. The environment directs this reconstruction in two ways: it endows certain genotypes with a realizable selective advantage by dint of its active role in ontogenetic development, and it selects against those genotypes lacking the capacity to capitalize on the potential guiding of development by the environment. By enacting this dual role of selective agent and ontogenetic guide, the environment shapes the population genotype in such a way that the final step in the process of genetic assimilation--the occurrence of a mutation or recombination which "substitutes" for the environment's role in development--becomes extremely probable.

Yet, while genetic assimilation is certainly a part of the solution to the problem of adaptation, it leaves the most enigmatic questions pertaining to this problem unanswered. In discussing the problem of adaptation it is helpful to follow Waddington in distinguishing exogenous from pseudo-exogenous adaptations. He describes the former as that category of adaptations "in which an animal living under particular circumstances, or behaving in a particular way, itself becomes modified so as to be better fitted for its special circumstances." Examples include the strengthening of muscles with use, the callousing of skin upon its repeated rubbing, the hypertrophy of one kidney upon removal of the other. Waddington describes pseudo-exogenous adaptations as those adaptations "in which the animal exhibits characteristics similar to effects which can be called forth as direct exogenous adaptations, but which on investigation are shown to be hereditary, and independent of any particular environmental influence." Examples include the thickened skin on the soles of humans' feet, the callosities on the underside of ostriches' bodies (located so as to cushion the bird while sitting), and the flattened second molar of the dugong, used for mastication, which appears to have been much more conical in this animals' evolutionary past.[25]

It is clearly pseudo-exogenous adaptations which lend themselves naturally to explanation by genetic assimilation. Waddington admits that genetic assimilation fails to illuminate the origin of _exogenous_ adaptations. Yet he fails to recognize that an indepth understanding of the processes of pseudo-exogenous adaptation must be premised upon a prior understanding of the processes of exogenous adaptation, and that the failure of genetic assimilation to clarify the latter is a fundamental limitation of this theory.

Consider, for example, the genetic assimilation of a threshold trait which Waddington worked with experimentally--crossveinless wings in _Drosophila melanogaster_. In his experiments Waddington subjected _Drosophila_ pupae to heat shock and consistently selected and bred from crossveinless adult flies. After 23 generations of treatment and selection, he found that an unusually high percentage of flies in the selected line developed crossveinless wings even in the absence of heat shock treatment; the trait had been genetically assimilated. Presumably, a process like that illustrated in Figure 2 had occurred. The environmental stimulus--the heat shock--directed the ontogeny over a threshold into a selectively favorable "canal," and the obstructing col was eliminated in many small steps in the course of selection.

Yet how pertinent or informative is such an experiment to the problem of adaptation in nature? This experiment, like most of those conducted by Waddington on genetic assimilation, involved artificial rather than natural selection. Because of the artificial selection regime, there is _perfect coupling_ of the developmental and selective roles played by the environment; the environmental arrow in Figure 2 pushes the developmental ball precisely where it should be pushed for optimal adaptation. The artificial selection regime ensures, _a priori_, that the organism will react to the environmental stimulus with the optimal response, i.e. an impeccable ability of the organism to adapt, _exogenously_, to the environmental stimulus is produced as a by-product, an artifact, of the experimental set-up. It is patently absurd to expect this kind of situation in nature; there is no reason to expect the ontogenetic-somatic and selective effects of the environment to be automatically coupled. For example, to pose a purely hypothetical case, it is implausible to postulate that the first primate to descend from the trees would have the capacity to respond to pressure on the bottom of the feet with adaptive callousing, unless, of course, such a capacity had been evolved in response to similar pressures in the arboreal environment.

Clearly, the possibility of genetic assimilation of a trait is always contingent upon an initial ability to adapt, exogenously, to the appropriate environmental stimulus. Yet, in nature, this exogenous adaptability must be the product of selection that occurred prior to selection of the kind which is illustrated in Waddington's experiment, i.e. selection must produce a capability of exogenous adaptation before pseudo-exogenous traits can be produced by the dual selective and ontogenetic processes of genetic assimilation. Thus, _in_

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25. Waddington (1975), p. 30.

nature, in the initial selective process which shapes the epigenetic landscape in such a way as to enable exogenous adaptation to a particular environmental stimulus (digging the "canals" where the environment pushes the ball), the selective and developmental roles of the environment are not coupled. The greater part of the complex process of shaping the epigenetic landscape must occur by random mutation and selection, unaided by an environment whose developmental effects complement its selective pressures, in true statistical random search "neo-Darwinian" style--Waddington, at least, offers no alternative.[26]

Waddington did conduct (at least) one genetic assimilation experiment which involved natural rather than artificial selection. This experiment,

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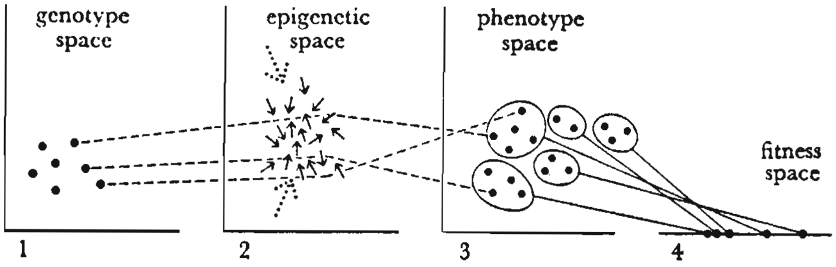
[26] In an article entitled "Does Evolution Depend on Random Search?" (1975, pp. 183-192), Waddington separates molecular evolution from morphological and physiological evolution, stating that while random search may in fact account for molecular evolution, "we certainly do not have to suppose that a vertebrate eye, the leg of a horse, or the neck of a giraffe is in any important sense the result of random search." Genetic assimilation is invoked in support of this contention. Waddington argues that while the occurrence of any mutation is random with regard to selection pressures, its effects need not be, for both the environment and the coordinated system of development of the organism will determine, to some extent, the phenotypic manifestations of the mutation. This is illustrated in Waddington's figure 5.



> Figure 5. Illustration of the process of natural selection in higher organisms. We start with a population of genotypes in a multidimensional 'genotype space' (1). These are mapped through a multidimensional space of epigenetic operators (2) (operators arising from the environment are suggested by dotted arrows), into an also multidimensional space of phenotypes (3). This is then mapped, by some complex function, into an essentially one-dimensional 'fitness space' (4) in which the only variable is the coefficient of fitness, or Malthusian parameter, i.e. the number of offspring produced. It is in the fitness space that natural selection acts; but the fitnesses which are within a tolerance limit of one another are in practice indistinguishable. (1975, p. 18)

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Yet (and this is precisely the point already stressed) Waddington has completely ignored the question of how those epigenetic and environmental operators came to be coordinated in such a way as to direct ontogenesis towards an adaptive end, and genetic assimilation, as discussed earlier, is impossible unless there is such an *a priori* adaptive coordination of the epigenetic operators (or the epigenetic landscape) and the developmental effects of the environment. The initial evolution of this coordination must depend on "random search"--again, at least Waddington offers no alternative.

however, does not respond to the criticisms just raised. In the experiment, the selective regime was provided by an unusually salty medium which killed most of the Drosophila larvae grown up on this medium. Waddington selected several strains for ability to grow and develop on the medium, breeding from the survivors for 21 generations. He then compared the ability of the selected strains to survive on mediums with high salt content to the ability of unselected strains to survive on this medium. Waddington reports, "The selected stocks became somewhat more tolerant of high salt concentration, though the difference was not very great. However,...there is no doubt that some genetic variability exists in the capacity of the animals to adapt themselves to the environmental stress and that this genetic variability has been utilizable by the natural selection employed"[27] thus giving rise to some genetic assimilation of this particular adaptive mode. The important point, however, is contained in the first statement; the results indicate that even the unselected strains possessed a substantial capacity to adapt (exogenously) to the stringent medium. In Figure 4 the shape (not level) of the curves represents the adaptability of the strains (adaptability = capacity to develop somatic adaptation to environmental stress): a rising curve indicates appropriate response to increased salt concentration.

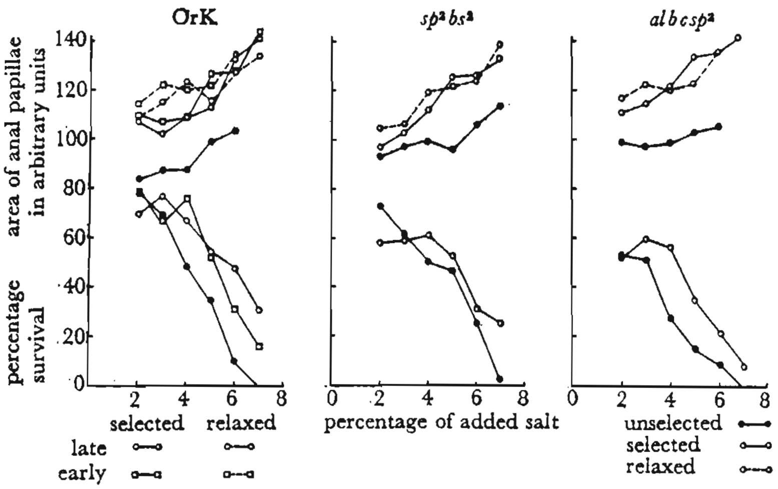

Figure 4. Selected and unselected strains in three stocks of D. melanogaster, in relation to the salt content of the larval medium. Above, the size of the anal papillae at various concentrations, in units derived from micrometer measurements. Below, the percentage of adults appearing from a given number of eggs. For the wild-type stock, two selected strains were prepared, one selected also for early emergence and the other for late. The papillae of the selected stocks were measured both in larvae derived from parents grown in the selection-medium (seven per cent added salt) and in 'relaxed' lines in which there had been one generation on normal medium between the end of the selection and the setting-out of larvae on the various concentrations. (Waddington, 1975).

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27. Waddington (1975), p. 47.

While Waddington claims that, "to some extent," the shape of the curves of the selected and unselected strains are different, they clearly appear quite similar. All the strains had a significant ability to adapt exogenously to the stringent medium before the experiment was initiated; this adaptability was not a consequence of the selected regime of the experiment. If an ability to survive in salty mediums was discovered as a pseudo-exogenous adaptation in wild Drosophila, Waddington's experiment would not explain the evolution of this adaptation; again, his work does not touch on the evolution of the ability to adapt exogenously to the environment, an ability which must be present in a population before genetic assimilation can occur.

Given that the efficacy of genetic assimilation is so clearly premised upon an initial exogenous adaptability, it is rather peculiar that Waddington could claim genetic assimilation as the "solution" to the problem of adaptation while blithely admitting that, as far as an explanation of the evolution of exogenous adaptations is concerned:

> At present, we hardly seem able to do better than produce ...the general argument--too general to be very satisfying --that it is an advantage to animals to be able to adapt successfully to new circumstances, and therefore natural selection will have favoured those animals which by chance had a hereditary endowment which enabled them to do so.[28]

The above discussion reveals the production of exogenous adaptations to be at the heart of the problem of adaptation. Waddington accomplished the partial clarification of the much less enigmatic phase of the adaptation process.

Furthermore, how much insight has Waddington offered into the mechanism of the latter phase in the evolution of heritable adaptations--their genetic assimilation? Waddington's clearest expositions of the process of genetic assimilation take his visual model of the epigenetic landscape, which is, in essence, a system of canals, as a point of departure. Yet this whole explanation system is a two-dimensional topographic schematization of developmental processes which are in reality multidimensional, as Waddington is the first to admit. The central element of the explanation system, canalisation, is accordingly a highly abstract concept which, in itself, offers no clues into the remarkable biochemical coordination system it "describes." The limitations of the canalisation model are most clearly illustrated when one attempts to apply it to the problems of complex coordinated adaptive physiological or morphological systems, such as the eye, or the front limbs of the pangolin. (The pangolin's front limbs are used for digging and accordingly require appropriately coordinated muscular, morphological, and antomical structures.) The evolution of such coordinated systems represents one of the anathemas to a random mutation—selection approach that ignores epigenetic processes, and Waddington states that the role of genetic assimilation in evolution becomes increasingly important "the more one is dealing with evolutionary changes in complex organs or organ systems which must be affected by numerous genes which have to be integrated with one another."[29]

Yet, when dealing with complex developmental systems which coordinate internal and external epigenetic interactions, the dimensionality of the coordinating mechanism is extremely high, and the canalisation terminology and epigenetic landscape models, which are two dimensional abstractions, lose whatever schematized explanatory power they had to offer. Waddington himself recognized this:

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[28] Waddington (1975), p. 47.

[29] Ibid., p. 28.

> When only a single (environmental) stress is involved and the response of the developing system shows a certain approximation to an all-or-none character, as in the temperature - shock or ether treatment experiments, one can represent the system by a diagram involving a single col or even a sharply defined threshold. When one considers the more complex stresses which arise in real life, such a representation becomes more difficult and also more artificial.[30]

So the very class of problems which, as Waddington recognizes, present the greatest difficulty for the neo-Darwinian paradigm, and which Waddington cites as evidence for the fundamental importance of genetic assimilation in evolution, are those very problems for which Waddington's canalisation model is least satisfactory, and for which the process, the mechanism, of genetic assimilation is thus least clear.

To put Waddington's contribution with respect to the problem of adaptation in perspective, consider the following summary:

The evolutionary process which goes the route of genetic assimilation occurs in two stages: A) Within a population, genetic change and selection lead to the evolution of an epigenetic system which enables exogenous adaptations to certain environmental stimuli; B) Some individuals within the population will be endowed with greater exogenous adaptability than others, and selection will act on this variability molding the population's genetic structure in such a way as to render it probable that the adaptation will eventually be genetically assimilated.[31] Waddington's work does not touch on the crucial initial stage of the evolution of adaptations, for genetic assimilation can, at best, enter into the latter part of stage A, when some coupling of the environment's selective and epigenetic roles has been effected--again, the two "stages" are not discrete. Waddington is responsible for recognition of the important second stage of the process, and his epigenetic models, particularly his concept of canalisation, are somewhat helpful in understanding the mechanism of genetic assimilation. Yet, when dealing with the complex adaptations which pose the greatest problems for neo-Darwinian evolutionary theory, Waddington's epigenetic visual models and the canalisation concept offer very little insight into the nature of the process of genetic assimilation. His topographic explanation system is a two-dimensional simplification of processes clearly of much higher dimensionality, and is therefore too simplified to serve as a useful model for understanding the nature of the genetic (and resulting epigenetic) restructuring which underlies genetic assimilation.

While Waddington has surely enriched evolutionary theory by introducing the concepts of genetic assimilation and developmental canalisation, the depth and range of application of these ideas is stringently limited. Yet Waddington poses them as a solution to the problem of adaptation, and the basis of a new "post-neo-Darwinian paradigm." This paradigm supposedly escapes the "neo-Darwinian" dilemma: the necessity of accounting for the apparent directedness, or telic quality, of evolution with an evolutionary process built upon the purely random reshuffling of nucleotide sequences and a non-teleological natural selection. Waddington states that whereas "the import of the previous ("neo-Darwinian") evolutionary theories can be sloganized by Jacques Monod's phrase 'Chance and Necessity,' the post-neo-Darwinian paradigm would substi-

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[30] Ibid., pp. 55-56.

[31] The two-phase description is purely schematic. The establishment of complementarity between the developmental and selective roles of the environment must occur gradually; the two "phases" are not wholly discrete.

tute slogans such as 'Learning and Innovation,' or 'Adapting and Improvising,' or, if you like a more with-it jargon, 'Recompiling and Heuristic Search.'"[32] This verbiage is exaggerated. Despite his proclamations of paradigm reformulation, Waddington provides no articulate comprehensive alternative to the "random search" model of evolutionary adaptation.

A CRITICAL ANALYSIS OF WADDINGTON'S EVOLUTIONARY THOUGHT: PART II: OTHER EVOLUTIONARY PROBLEMS

Epigenetic concepts--particularly, perhaps, canalisation--have important implications for a wide range of evolutionary issues. Yet, while Waddington did employ epigenetics in telling criticisms of the "neo-Darwinian paradigm," genetic assimilation appears to be Waddington's sole concrete positive contribution to evolutionary theory. With the exception of the theory of genetic assimilation, Waddington did very little to show how epigenetic ideas could be constructively integrated into evolutionary theory. In countless articles, Waddington utilizes general epigenetic principles to criticize the premises of the "neo-Darwinian paradigm," offers genetic assimilation as the foundation for an alternative view of the evolutionary process, and does little else. In the 1940s and 1950s evolutionists were struggling with a broad array of challenging problems--from bradytely and tachytely to vestigial organ retention. Yet, despite the relevance of epigenetics to many of these issues, few find more than passing mention in Waddington's work. In 1956, Julian Huxley reviewed Waddington's monumental Principles of Embryology. He states:

> My most general comment is that, although Waddington has done so much to link epigenetics with genetics, he has not proceeded to make the further link with evolution.[33]

Huxley's comment applies, not just to the Principles of Embryology, but to the majority of Waddington's work (again with the exception of those works dealing with genetic assimilation and canalisation). When Waddington did touch upon such problems, his treatment was generally cursory, and couched in rather vague and general terms. Waddington did not, generally speaking, develop his ideas into predictions, explanatory statements, or even questions (easily testable or otherwise) pertaining to a specific evolutionary context. In a little article, "Epigenetics and Evolution," Waddington does go so far as to isolate three specific problems which he believes are inadequately dealt with by modern evolutionary theory, and attempts to illustrate how epigenetic awareness may throw some new light on these questions. Yet even here his treatment is rather superficial.

Waddington spends the bulk of the article discussing the problem of adaptation, and Waddington's proposed "solution" of genetic assimilation has already been discussed at length.

The second problem Waddington discusses is that of "the nature of the differences between species or species groups." He states,

> Goldschmidt, in particular, has argued that in nature certain fairly large groups of forms differ from each other in some way which is not directly comparable to the manner in which the local races of a single species, or the species of a single species group, are related.

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[32] Waddington (1975), p. vi.

[33] J. Huxley, "Epigenetics: [A Review of] Principles of Embryology," Nature 177 (1956): pp. 807-809.

> He has spoken of an 'unbridgeable gap' between such major groupings...It certainly seems to the present author that we are very far from having heard the last word on the nature of the variations on which interspecific differences depend.[34]

In addressing this problem, Waddington states,

> As regards the notion of an 'unbridgeable gap' between related species groups, it is sufficient to point out that some such idea becomes almost a necessity as soon as we think of development as a cybernetic process, involving stabilization through feedback and similar mechanisms. Any system of such a kind must be regarded as to some extent organized, and although an organized system may be capable of some degree of continuous variation around a mean, it cannot in general change through a continuous series of stages into another system of organization. The latitude of possible continuous variation and the sharpness of the transition from one organizational system to another will probably vary in different cases. There is however, nothing unexpected if it is found that the epigenetic systems of the members of a genus exhibit a number of relatively distinct alternative forms, to each of which a certain, but restricted, field of variation is open. It is suggested that it is in such primarily developmental terms, rather than in narrowly genic considerations, that an explanation for the existence of species groups is to be sought.[35]

This statement, while provocative, hardly goes very far, and Waddington did nothing to concretize his arguments. To my knowledge, the ideas contained in the quoted passage are not even reiterated in any of Waddington's other publications. He did not, as he might have, use these ideas to criticise such articles as Mayr's 1954 paper, "Change of Genetic Environment and Evolution," an attempt to explain species group differences on rather "narrow genic grounds." Left in an undeveloped and general form, Waddington's contention that the existence of species groups should be investigated in primarily developmental, rather than genetical, terms is of little use to the field taxonomist; nor is it even immediately convincing. Mayr sounds very Waddingtonesque in discussing sibling species:

> Systematists (including paleontologists) still tend to correlate too closely the amount of phenotypic difference with the amount of genetic difference. The category of sibling species proves that such an equation neglects to allow for manifestations of developmental homeostasis. The occurrence of such species proves that major construction of the genotype can take place without any visible effect in the phenotype. The capacity of such species for developmental homeostasis must be so great that any unbalancing genetic change is at once compensated somewhere along the developmental pathway.[36]

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[34] Waddington, "Epigenetics and Evolution," <u>Symposia of the Society for Experimental Biology</u> VII (1953): p. 188.

[35] Ibid., p. 198.

[36] E. Mayr, <u>CSH Symposium</u> 24 (1959): p. 12.

Yet, if Mayr's interpretation is correct, are not "narrowly genic considerations" of paramount importance in understanding the taxonomic problems associated with sibling species?

Lastly, Waddington addressed the third "major question mark in evolutionary theory"--the adequacy of existing explanations for the range of evolutionary rates--from bradytelic to tachytelic--in evidence in the fossil record:

> Again, in consideraing the rate of evolutionary change and diversification in various groups, it may be that the idea of epigenetic canalisation provides a useful category of thought which has so far been overlooked. A canalised system is one which is difficult to alter...the epigenetic system itself may have become such a complexly interwoven nexus of cybernetic interactions that it is either extremely difficult to produce any phenotypic change at all, or the only possible changes may involve such a complete disruption of the epigenetic organization that the phenotypes produced are highly aberrent and thus probably at a strong disadvantage. It must be admitted that we know as yet very little about the strength of the canalisation in different forms, but perhaps enough has been said to indicate that it is at least a concept which it may be well to bear in mind.[37]

Again, there is an interesting idea here, and because of the nature of the phenomenon being discussed, it is perhaps difficult to see how Waddington could have done much more than speculate along the lines of the quoted passage. Yet, surely one of the three "major question marks in evolutionary theory" deserves a little less cryptic speculation. Schmalhausen, in 1939, devoted a whole article (in Russian) to "The Significance of Correlation in the Evolution of Animals," the fundamental theme of which is presumably captured in the following quotation from his book, Factors of Evolution:

> ...the rate of specialization (in the evolution of higher forms of life) is definitely limited. The transcendence of this limit, which involves the production of unharmonious nonadaptive forms, causes an excessive development of parts, gigantism, and extinction (Schmalhausen 1939). This limit, apparently, is set by the relative slowness of the transformation of the correlation system without which progressive evolution is practically impossible (Schmalhausen, 1939).[38]

Mayr concretizes these ideas somewhat by applying them to bradytelic evolution in horses:

> Even a gene mutation which leads to an improvement in the phenotype may have difficulties in such a system because it will take a long period before it is fully fitted into the total pleiotropic buffered gene-complex. Simpson's findings that the tooth elongation of fossil horses was of the order of only one millimetre per one million years is a suitable illustration of this process. To be of real value such an improvement in the teeth has to be correlated with a strengthening of the upper and lower jaw and with numerous other readjustments of the skeleton, the muscles, and presumably even

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[37] Waddington, "Epigenetics and Evolution," p. 198-199.

[38] I. I. Schmalhausen, Factors of Evolution (Philadelphia: The Blakiston Co., 1949), p. 279.

> the viscera and the nervous system. All these changes require a rather thorough overhauling of the total gene complex. It is not often that selection permits a single structure to rush far ahead of the other parts of the system to which it belongs.[39]

This explanation, however, is not terribly convincing. If valid, it would predict that bradytelic evolution was the rule in the evolution of higher forms of life, and leads to difficulties in understanding tachytelic evolution. Mayr later offered an alternate explanation for bradytelic evolution. Picking up the theme of his discussion of sibling species, he suggested that "developmental homeostasis is so highly developed as to prevent completely the phenotypic penetrance of the concealed genetic changes." He goes on to discuss tachytelic evolution along the same lines:

> One might utilize the same phenomenon of developmental homeostasis to explain the diametrically opposite evolutionary phenomenon, the sudden, sometimes almost explosive, breaking up of morphological types....None of the explanations that are usually advanced...are particularly convincing. It would seem more likely that some special event such as a sudden shift in ecological balance or the rare occurrence of a successful hybridization has led to the upsetting of the developmental homeostasis and has permitted new selective forces to act upon the newly available phenotypic variation.[40]

The important point, again, is that Waddington did not really explore the evolutionary implications of his epigenetic ideas as thoroughly as they deserved, or, in some instances at least, with the same degree of insight or detail that other evolutionists did. That pressing evolutionary questions are often given short shrift in Waddington's writings is certainly evident in The Strategy of Genes, Waddington's most important work on evolution—related problems. In this book, Waddington again identifies the same three deficiencies in modern evolutionary theory, but the problems of "unbridgeable gaps" and evolutionary rates are hardly discussed at all--Waddington does not even repeat the preliminary ideas quoted from "Epigenetics and Evolution."

A closer look at one aspect of the last Mayr quotation lends further support to the contention that Waddington failed to exploit the evolutionary potential of his developmental ideas. Mayr's argument hinges upon the idea that a highly coordinated developmental system possessing homeostatic properties may allow a build-up of genetic variability within a population. This poinw was heavily stressed by Schmalhausen in Factors of Evolution:

> The system of regulative correlations also provides normal morphogenesis with a certain degree of protection against disruptions by large hereditary variation, namely mutations. The process of mutation becomes concealed to some extent; this favors unhindered accumulation of numerous mutations and formation of a large reserve of hereditary variability. This reserve can be readily mobilized during changes in the external environment and is one of the fundamental conditions for high evolutionary plasticity of organisms. Accordingly, the progressive development of regulating mechanisms steadily

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[39] E. Mayr, "Change of Genetic Environment and Evolution," in Evolution as a Process (London: George Alen, 1954): p. 166.

[40] E. Mayr, CSH 24,p. 13.

> increase the plasticity of higher animals and provides basic conditions for further evolution at an accelerated rate.[41]

This hypothesis hits at a fundamental question in evolutionary theory: mechanisms for retention of genetic variability. If the importance of the described mechanism in nature approaches that attributed to it by Schmalhausen, the implications for evolutionary theory are profound. For example, the assumption that a population subject to consistent, stiff selection pressures will have its store of variability rather drastically reduced is important in Sewall Wright's thinking, especially the evolution of his "shifting balance" theory of evolution. Wright's premise is supported by animal breeding work (Wright's own area of experimental expertise) but its general validity in large natural populations is open to question. It must also be kept in mind that traits investigated in the laboratory (for example, coat color) are often those least likely to be those with a strongly canalised or buffered development (Waddington).

The point that developmental buffering can lead to a storage of genetic variability and thus provide a population with evolutionary plasticity is by no means a major theme in Waddington's work. He does mention it in at least one passage in The Strategy of Genes, but certainly does not lend it the emphasis its evolutionary significance deserves. His failure to question Wright's assumptions along the lines indicated reveal, perhaps, that even in his criticisms of mathematical models Waddington did not employ his epigenetics as extensively as he might have, and his criticisms are accordingly less effective than they might have been. In discussing the weaknesses of mathematical models Waddington did not, in general, go much beyond stating that the model assumption of one-to-one correlation between genotype and phenotype was highly unrealistic; he did not clarify, explicitly, how his epigenetic ideas could indicate that the "tempo and mode" of evolutionary processes might be qualitatively different from that implied in, for example, Wright's models. To wit; he never stated bluntly: Wright's mathematical models supposedly show that variability in an intermediate or large panmictic population with no immigration is severely depleted by strong consistent selective pressures therefore rendering continued evolution difficult, but the phenomenon of developmental buffering renders this conclusion, and all deductions from it, somewhat dubious.

Theories of epigenetics could be applied to many evolutionary questions other than those already discussed. Waddington again did not take the initiative in these other directions, but other evolutionists did. Thus Dobzhansky applies the concept of developmental buffering in discussing gene homology:

> Genes so canalize the physiological processes that the egg, the embryo and the adult body develop in certain species-specific and genotype-specific ways. The presence of homologous organs is, then, not necessarily good evidence of persistence of identical, similar or even homologous genes.[42]

Later in the same article Dobzhansky explains how the complexity and interdependence of developmental processes may provide explanations for such phenomena as vestigial organs, which are difficult to explain from a "bean bag" perspective:

> Vestigial organs need not be determined by vestigial genes. They are rather by-products of developmental processes which

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41. Schmalhausen, Factors of Evolution, p. 283.
42. Dobzhansky, CSH 24, p. 23.

> bring about the appearance of vestigial as well as of non-vestigial organs and characters....What advantage would the organism get from so modifying its development that the vestigial organ will be gone but the rest of the development will remain unchanged? If there existed a one-to-one relation between a gene and a trait (as classical geneticists liked to assume) then a vestigial organ would make a gene unnecessary and it would disappear. But the situation is really different: evolution does not consist of independent changes of organs or traits; what changes is the genetic system and the developmental system which rests on it.[43]

Lerner (1959) questions the generality of results obtained from experiments on the genetics of any particular natural population, still harping on the lack of a one-to-one correlation between genotype and phenotype:

> Identical phenotype expressions of two individuals from different gene pools, both of which may be at adaptive peaks, may be based completely on different genotypes and developmental processes. The sequential nature of evolutionary changes produces an immense variety of solutions to similar problems of adaptation, a fact which precludes single and universally valid explanations of observations on the population level.[44]

This statement is a little too general to be very satisfying, but it does at least broach an important issue, which again Waddington did not address.

These examples have been cited to show that while epigenetic ideas certainly have a great deal to say about evolution, Waddington himself said very little of it. Again, he did not, in general, develop his ideas into predictions, statements, or questions pertaining to particular evolutionary situations. Without such concretizing examples, all but the most general and theoretical evolutionary implications of epigenetics remain unclear. A brief look at the evolutionary contribution of the mathematical models Waddington was so fond of criticising may serve to concretize these contentions somewhat by illustrating more precisely what Waddington did not do.

Waddington offered some of the most sophisticated criticisms of the mathematical models of Fisher, Haldane, Wright, et al. For example, in discussing Wright's theory of drift, he states,

> Sewall Wright...is well aware of the artificiality of attaching fixed selective coefficients to individual genes) and has, in fact, provided several discussions (of genetic drift) which are couched in broader terms and take account of the necessity to argue in terms of complete genotypes rather than individual alleles. However, in order to do this one has to be content with expressing the various possibilities in a qualitative manner. Wright, in fact, describes them in terms of a multi-dimensional phase space of gene frequencies.... Such a mode of expression can be very valuable in providing a set of terms--or even a visual model--in which one can work out ideas which are otherwise difficult to formulate. In connection with the particular problem of drift, however,

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[43] Ibid., p. 27.

[44] Lerner, CSH 20, p. 336.

> it loses touch with the point which is of crucial importance, namely the quantitative. Even if we are content with the simplest formulations of the mathematical theory which yield explicit algebraic expressions containing [parameters of population size, selective pressure, migration, etc.], we can in practice hardly apply then, since the quantities concerned are exceedingly difficult to measure under natural conditions; while if we proceed to a more profound and convincing theoretical account of the situation, even any explicit reference to the parameters disappears and we find ourselves left with nothing which will help us to decide how important the process of drift will be in Nature.[45]

This is certainly an eloquent argument. Yet while it must be admitted that Wright's mathematics cannot "solve" the problem of the role of random drift in evolution, it cannot be forgotten that his mathematical work did raise and focus attention on this issue, which is of great importance for evolutionary theory. Furthermore, Wright's work (among others') did identify and highlight the crucial importance of certain parameters (such as population size and migration) in evolutionary processes, and in so doing guided some of the field work which became so important in evolutionary theory (Dobzhansky's working relationship with Wright exemplifies this). Waddington's theoretical ideas certainly did not serve a similar purpose. To a certain point, this can be attributed to the enigmatic nature of developmental process. Parameters such as population size and gene frequency can be identified, quantified (at least theoretically), and utilized in evolutionary calculation. The identification, let alone quantification, of the aspects of developmental system pertinent to evolutionary process is more problematical. Nevertheless, it is not necessary to formalize ideas mathematically in order to make predictive statements about particular evolutionary circumstance. Waddington, however, did not do this. While Waddington's criticism of Wright's mathematical work is very telling, and he is certainly correct in stating that Wright's fitness surfaces discard any reference to identifiable parameters, much of Waddington's work is open to the very objections he raises in criticising Wright. The corpus of Waddington's work represents an attempt to "proceed to a more profound and convincing theoretical account of the [evolutionary] situation," yet he virtually never makes explicit reference to particular parameters, and, in viewing Waddington's evolutionary thinking as a whole, we are left with very little which will help us decide to what degree, and in what ways, epigenetic processes are important for evolutionary theory. Waddington's claims of comprehensive paradigm reformulation are insupportable.

This judgment, of course, by no means necessitates unequivocal rejection of the evolutionary ideas and directions sketched in Waddington's work. In fact, it may not be amiss to suggest that Waddington's theory contains important elements of a coherent conception of evolutionary system the full articulation of which is yet to be achieved.

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[45] Waddington, The Strategy of Genes, p. 84.