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Article in *Biology and Philosophy* · January 2006

DOI: 10.1007/s10539-004-0319-7

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*Book review*

## **Genes as followers in evolution – a post-synthesis synthesis?**

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A review of Mary Jane West-Eberhard, *Developmental Plasticity and Evolution*, 2003, Oxford University Press, New York.

The “Modern Synthesis” of evolution, forged in the 1930s and 1940s, is widely acknowledged to have been incomplete. Developmental biology was left out. It was hoped that this gap would soon be filled, and that more knowledge of developmental genetics would ultimately allow the integration of developmental biology and evolutionary biology. But despite the great explosion of data in molecular developmental genetics during the past two decades, the expected synthesis still has not taken place, although some interesting insights have certainly been gained. Instead, an increasing number of biologists have begun to suspect that a synthesis between developmental and evolutionary biology will require a new approach rather than simply more of the same – more genetic data.

West-Eberhard’s book *Developmental Plasticity in Evolution* is an attempt to present the long-awaited synthesis between developmental and evolutionary biology. She takes the view that a different approach is indeed needed, and her point of departure is not the gene, but the phenotype. It is phenotypic continuity across generations, and the plasticity of the development of the phenotype, with its multitude of transformations and adjustments, which are the raw material for natural selection. In her massive volume, West-Eberhard (henceforth W-E) examines the role of plasticity in adaptation, and shows how a view of evolution that focuses on phenotypes changes how one approaches some of the major problems in evolutionary biology. The result is a rich synthesis of data and ideas from all branches of biology. In this review I shall examine and discuss the structure of her main arguments, and see in what ways they provide an alternative to the traditional, no-longer-modern synthesis.

**The scheme of the book**

“The central theme of this book is the evolution of phenotypes – the expressed characteristics of living organisms. I define evolution as phenotypic change *involving* gene frequency change, not just gene frequency change alone. I want to know what makes the phenotype change during evolution: how does change start and how do the genes get involved? The central argument I will make is that the secret to understanding evolution is to first understand phenotypes, including their development and their responsiveness to the environment. Of course, development and responsiveness involve genes, as does evolution. So I attempt to tie all of these things together – development, responsiveness, genetics, selection and evolution – in a single scheme”. (p. 28, W-E’s italics).

The book has four parts. In the first, “Framework for a synthesis”, W-E discusses the nature of developmental plasticity and the organization of the phenotype. She argues that since developmental processes, which are inherently plastic, produce the phenotypic variations that are screened by selection, this must be the starting point of both developmental and evolutionary analyses. She believes that the organization of the phenotype is essentially modular. According to W-E, an adaptive novelty starts as a developmental change that occurs within the structure of a pre-existing phenotype and is reproduced every generation. The novelty is associated with the restructuring of the developmental units: the deletion, amplification, temporal and spatial re-organization of body parts, stages in the life-cycle, etc. A developmental innovation can originate in two ways, which are not mutually exclusive: either as a new mutation, or through recurrent environmental induction. The latter is considered by W-E to be the more common and the more important. Genetic changes, which fine-tune the new developmental adjustments, will be selected if such fine-tuning is adaptive and the inducing environment persists for long enough or is recurrent. Genetic variations that have adaptive effects are, therefore, usually followers, rather than leaders, in evolution.

W-E maintains that thinking about a phenotypic novelty as the outcome of plastic development simplifies the explanation of many evolutionary phenomena. Evolutionary novelty, from this point of view, is seen as the result of phenotypic recombination – the formation of a variety of new (heritable) phenotypes that are combinations (in space and time) of semi-autonomous modular traits. The discussion of the various types of phenotypic recombination, and hence the discussion of the developmental origins of evolutionary novelty, are the subject matter part II of the book, “Origins of Novelty”. W-E claims that the evolution of all new traits, at all level of organization from proteins to behavior, should be seen as a result of such recombination.

The third part of the book, “Alternative Phenotypes”, discusses a subject central to W-E’s synthesis. Alternative phenotypes reflect alternative developmental options that are either displayed by the same individual in different

conditions, or by different individuals within the same population. They are typically condition-sensitive and are, therefore, underlain by differences in gene expression rather than gene-frequency differences (p. 380). Selection acting on the thresholds and patterns of gene expression can readily lead to an increase in plasticity, or to an increase in the occurrence of one particular expression pattern and the elimination of the other. Hence, alternative phenotypes may either remain and evolve as outcomes of condition-sensitive developmental paths, or, if environmental conditions become more uniform, one alternative may become fixed. The generation of alternative phenotypes (a result of an environmental or, less commonly, mutational change) leads to coordinated modifications of many aspects of the phenotype, and evolutionary changes based on these modifications may help explain various macro-evolutionary processes. This leads W-E to part IV of the book, “Developmental plasticity and the major themes of evolutionary biology”, which examines the consequences of her view for major problems in evolutionary biology. She shows how her perspective can offer elegant, sometimes alternative and often complementary, ways of thinking about evolutionary issues that are regarded as problematical – gradualism versus punctuation, the association between micro and macro evolution, adaptive radiations and the role of the environment in evolution, and finally, sexual reproduction.

### **The theoretical framework**

It is very difficult to do justice to the wide-ranging and detailed arguments presented in the book, but since my main objective is to discuss the basic theoretical structure of W-E’s synthesis and see in what ways it differs from the conventional view, it is necessary to try to summarize her arguments. I believe that the following summary is fair and accurate:

1. Organisms are inherently responsive. The normal response of an organism to a change in its usual conditions of life is a modification of its phenotype. A “change in conditions” may be a mutation with a visible effect, or, more commonly, a persistent or recurrent environmental change. All phenotypic responses and adjustments occur in a pre-existing developmental system, a pre-existing phenotype. All occur within the dynamic, plastic framework of phenotypic continuity.
2. A responsive, often adaptive, phenotypic change in an organism is the normal reaction to new challenges. We can see this clearly when we consider how we learn a new skill (for example, learning to read and write), or when we consider the morphological adjustment in bones and muscles that are the results of changes in mechanical pressures brought about by a change in diet. The responses to new conditions (a literate society, or a new diet leading to increased pressure on jaw-bones) are clearly *not* the result of direct past genetic selection for literacy, or direct selection for the new use of jaws. They

are novel developmental re-organizations, based on the general potentialities of the pre-existing genotype, that are induced by the new conditions.

3. The responses to changed conditions inevitably involve *phenotypic accommodation*, which adjusts the organism as a whole to the developmental change, so that it can flourish, or at least survive, in the new conditions. Developmental accommodations are mediated through general biological properties such as mechanical flexibility and the multiplicity of partially-overlapping regulatory elements, and through developmental processes such as selective stabilization at the cellular, physiological and behavioral levels. These processes lead to correlated changes in various aspects of the phenotype. The induced response and the phenotypic accommodation to it always come together.
4. The way that the plasticity underlying phenotypic accommodation is manifest depends on the basic organization of the phenotype. This organization is modular, and is delimited by developmental switches, which are defined as discrete changes in the state of an organ or the rate of a process. Modularity does not mean that there is no interdependence between developmental units – there is an inclusive hierarchy of units (several interacting, functionally-correlated, smaller units comprise a bigger unit), and at a given level of organization there are differing degrees of interdependence (some units are more autonomous than others), as well as continuous variation *within* the fuzzy boundaries of a unit. Phenotypic accommodation involves the re-organization of the modular units of development as well as some shifting of the module boundaries.
5. There is natural selection of those organisms that can respond in a plastic and functional manner to the new conditions. Some organisms differ in their ability to respond because there are differences in their genes, others because of where and when they encounter the new conditions, still others because of what they manage to learn, and yet others because they have received different, non-genetic, legacies from their parents. There will be selection among these variant, responsive organisms.
6. Evolutionary change happens when the basis for the selective differences between organisms is heritable. For W-E this means that such selective differences must be genetic. Genetic changes that stabilize the functional response (i.e., make it more reliable and precise), and/or that ameliorate detrimental side-effects, are selected. W-E terms such genotypic change *genetic accommodation*. Selection of genes is possible only because alleles become selectively relevant as a result of phenotypic accommodation. Since genetic accommodation follows phenotypic accommodation, genes, and changes in gene frequencies, follow rather than lead in the evolutionary process.
7. Focusing on the plastic and modularly-organized phenotype, and on the prevalence of environmentally-induced phenotypic novelties, provides a coherent way of describing evolutionary changes, a way that is based on the combinatorial possibilities that the blend of modularity and flexibility al-

lows. It also provides simple and plausible interpretations of many evolutionary processes, such as sympatric speciation, and allows a better understanding of major evolutionary phenomena such as adaptive radiations and punctuated evolution.

W-E shifts the focus of evolutionary analysis to the selection of inducible phenotypes and to the dual role of the environment in inducing (and hence developmentally constructing) new phenotypes, as well as selecting among them. This view is not new, but W-E's account provides the most comprehensive discussion of it and of its implications to date. Her approach highlights three major issues, which, when put together, do challenge the standard, gene-based way of thinking about evolution. The first is the nature of developmental plasticity and its relationships with canalization; the second is the nature of the persistence of new (usually environmental) conditions; and the third is the role of genes in evolutionary processes driven by environmentally-induced modifications.

### **The challenge of the two-legged goat**

Monsters (by which I mean extraordinary, usually morphological, phenotypes, although the inspired Hebrew-speaking biblical donkey would qualify too) have always been a source of fascination. When biological investigation began to be systematized in the 18th century, scientists like Maupertuis realized that the monsters manifest interesting regularities, and that these might assist in understanding normal development as well as heredity. For others, monsters created profound problems: when Linnaeus was brought a highly unusual morphological variant of the common toadflax, *Linaria vulgaris* (he named it "Peloria", after the Greek word for monster), it challenged his ideas about the fixity of species. Since then, spontaneously occurring "monsters", as well as environmentally and experimentally induced ones, have frequently been used to understand the nature of developmental options and the evolutionary possibilities that they may point to. Well known examples can be found in the writings of Darwin, de Vries, William Bateson, Goldschmidt, Waddington and Alberch, and these, as well as many others, are reviewed and discussed by W-E.

W-E continues the tradition of using monsters to highlight both developmental and evolutionary issues by discussing the case of the two-legged goat, which was described by Slijper in 1942. This famous goat was born without forelegs, adopted a semi-upright posture, and moved bipedally on her hind legs, hopping around somewhat like a kangaroo. After her untimely and unfortunate death (she was killed in an accident), extensive post-mortem examination revealed many coordinated changes in the goat's morphology, which were obviously the consequence of her unusual mode of locomotion. In addition to a changed hind leg and pelvic structure, she had a curved spine, unusually thick and large neck, and various functionally correlated changes in her skeleton and musculature.

The case of the two-legged goat case illustrates several important things. One of the most significant is that it shows that pre-existing genetic and developmental possibilities allow physiological adaptations that could never have been selected in the past. It is safe to assume that walking on their hind legs did not regularly re-occur in the evolutionary history of goats, and hence there could have been no pre-existing selected “genetic program” for the adaptive organization of a two-legged-goat phenotype. The example, therefore, highlights the way organisms make phenotypic adjustments to a new set of existential needs by re-organizing their subunits. Presumably, if such a case happened again, and we were able to examine the gene expression profile of the two-legged goat, we would see a corresponding re-organization at the molecular level. The restructuring of the pre-existing developmental system has potentialities at all levels of organization, but something different can be constructed only by exposure to new conditions. The potential to produce alternative phenotypes (plasticity) has a genetic basis only in the trivial sense that every biological property has a genetic basis: *it does not pre-exist as a genetic program selected to produce those phenotypes*. Hence, new conditions can lead to the developmental construction of truly new phenotypes, re-organizing the phenotype at all levels of organization. This re-organization utilizes the modular nature of the phenotype as well as the interconnectedness between the various subunits (hind legs, pelvic musculature and skeleton, thoracic skeleton).

The pathological and “monstrous” case of the goat is a good illustration of a plastic change that goes beyond that manifest in the range of conditions in which previous selection had occurred, but several additional points need to be made. First, not all extraordinary changes are pathological. For example, the bonobo Kanzi, who has the remarkable ability to comprehend spoken English with the proficiency of a two-and-a-half year old child, and is able to converse in a symbolic language, is certainly a very unusual ape, but few would regard him as pathological. There is little doubt that his unusual skills, elicited by a highly structured developmental and social environment, involve a completely novel re-organization of brain activity. Second, there is evidence that some gross adaptive phenotypic changes (mostly associated with behavior and diet), which are found in nature, can be induced experimentally by comparable conditions. One of W-E’s examples (p. 574–578) is the different jaw morphologies seen in species of cichlid fish, which can be experimentally induced by keeping them on diets similar to those of the fish in natural conditions. The third point to be noted is that many far less dramatic but nevertheless novel changes show the same type of newly re-organized adjustment. In all cases, the reconstruction of the phenotype that is elicited by the new conditions seems to precede any genetic tweaking. The input of the environment is highly specific, and is as essential as the input of genetic factors. (W-E gives many examples of this throughout the book, but see especially chapter 26.) The phenotypic change is the initial adaptive response, which can then be fine-tuned in many different ways by natural selection acting on the heritable components of the developmental systems.

The two-legged goat is a dramatic example of developmental plasticity, with interesting and varied evolutionary implications, which are thoroughly discussed by W-E (see particularly chapter 16). It also illustrates another point which W-E doesn't go into much, although it is relevant to her arguments, and that is the relationship between plasticity and canalization. Although the terms seem to be opposites, with canalization referring to phenotypic constancy and plasticity to phenotypic changeability, every case of canalized development in the face of genetic and environmental challenges requires plasticity at lower levels of organization. Thus, the increase in the number of red blood cells at high altitudes can be seen as a plastic response if we look at the number of red blood cells (which changes), but it is an illustration of canalization if we look at the concentration of oxygen in the blood (which remains constant). Similarly, a genetic change that does not lead to a different visible phenotype (evidence of canalization) may require a change in the expression of other genes (plasticity) to compensate for the gene change. Clearly, plasticity is not always evident at all levels – plastic changes may be seen only at the molecular level, with the morphological or behavioral levels being unchanged; alternatively, plasticity may involve additional levels of organization. Whether there is a change at a given level (e.g., in morphology) depends on the nature of the environmental or genetic challenge and on various constraints. Canalization can, therefore, be seen as the absence of developmental change at higher levels of phenotypic organization, which is underlain by plasticity at lower levels. Even with extreme cases such as the two-legged goat, the higher level – the *capacity* for locomotion – remained (functionally) unchanged, while morphology and behavior changed profoundly.

W-E rightly criticizes the dichotomy that is usually made between canalization and flexibility, and recognizes Waddington's appreciation of the relation between them (p. 25). However, she criticizes his strong focus on canalization, and attacks the visual metaphor that he used, the epigenetic landscape, claiming that Waddington gave undue weight to genetic factors in development, and that his landscape and accompanying text led to a view of development in which the effects of environmental change are seen as a disturbance of normal development. I think that she misreads the metaphor and underplays Waddington's repeated emphasis on the roles of the environment and developmental plasticity. Waddington believed that environmental changes can alter developmental paths and that this can lead to gross phenotypic change – indeed all his genetic assimilation experiments are based on the ability of environmental changes to alter phenotypes. Of course, he was greatly interested in the fact that very often the macroscopic attributes of the phenotype remain unchanged, despite changes in genes and the environment, and he tried to understand this constancy. Obviously this led him to focus on the evolution of this stability in the face of disturbance (completely new and stressful conditions are often experienced as a disturbance). However, Waddington certainly thought that phenotypic changes that result from environmental changes are common and extremely important in evolution. On page 103 of *The Strategy of*



*the Genes* (1957), Waddington illustrates his approach to the central role of the environment by contrasting two views of how evolution works, illustrated by two simple diagrams. The first diagram depicts the environment as determining the selective forces leading to the direct selection of genotypes, as well as introducing noise into development (the conventional view). The second diagram illustrates the view that Waddington adopted, and in words that could have almost been written by W-E, and certainly show the closeness of their views, he said: “In the second diagram, which represents in very simplified form the point of view being advanced here, the environment not only determines the selective forces, but also co-operates with the genotype in the specification of the phenotype; and it is on the latter that selection acts, its influence on the genotype being secondary . . . When we emphasize that selection operates on phenotypes which are the joint resultant of genotype and environment, it is in the context of adaptation that we naturally find ourselves, since we are in fact suggesting that all natural selection is in fact a selection for the ability of the organism to adapt itself to (that is, to develop into a fit form in) the environment in which it finds itself. In later chapters, some definite hypotheses will be drawn from such considerations, and some experiments bearing on them reported”. (pp. 103–4). The experiments he refers to are his famous genetic assimilation experiments, and the general hypothesis that he presented is that environmental induction, by leading to phenotypic change that is subsequently modified and fine-tuned by the selection of genes, is the most common initiating event in adaptive evolution. Viewed in the context of his extensive writings, I see Waddington’s visual metaphor of epigenetics as an illustration of a dynamic, complex, interactive process, and find it extremely useful, an aid in both thinking and teaching.

### **Environmental persistence, phenotypic recurrence, and the Lamarckian bogeyman**

W-E defines the environment broadly, and includes in the definition the external, the social and the internal environment (e.g., the milieu of the cell is the environment of the gene). Thus, “environment” includes all the contextual aspects that are external to the focal unit. As she stresses throughout the book, the persistence of the environment can lead to the continuous construction of alternative phenotypes, which are the raw material for selection and the point of departure for most evolutionary processes. This very basic and important point is closely related to another that is of fundamental importance – the continuity of the phenotype and the recurrence of novel phenotypic variations. Every mutational effect, like every environmental effect, occurs in the context of a pre-existing dynamic system, which is the result of an unbroken chain of phenotypes. What is passed on from one generation to the next are many components of the phenotype, not just the genetic component (e.g., proteins and RNAs are also transmitted). All these components have to be considered

when we try to understand the effect of a change in the conditions of life on development, and genes have no primacy as causal agents when we consider development. However, when thinking about evolutionary change, the focus has to be on the *trans-generational recurrence* of alternative phenotypes. In other words, there must be transmission of phenotypic variations between generations, and evolutionary change involves a change in the frequency of such transmissible (or heritable) phenotypes. The question to be asked is what types of persistence allow the re-occurrence of a particular developmental variation for generation after generation?

I think it may be useful to summarize the main features of the different types of persistence, since this may clarify their roles and highlight W-E's curious neglect of some of them as *direct* agents of evolutionary change.

- Genetic persistence, which depends on the replication of genes and allows the transmission of variations in genes.
- Environmental persistence that is independent of the activities of the organisms. For example, a climatic change such as an increase in temperature that persists for many generations and repeatedly induces a new phenotype.
- Environmental persistence that is dependent on the activities of the organism and, to a large extent, is the result of such activities. All the examples of trans-generational niche-construction belong to this category. The most obvious examples are behavioral – through social learning, certain behaviors in a group of animals may persist for many generations and lead to the formation of traditions. Different traditions may occur in different groups without genetic change.
- Developmental persistence that depends on physiological feedback loops that re-generate the initial developmental conditions. An example is the persistence of a male-biased sex ratio in some Mongolian gerbil lineages, which is the result of interactions between testosterone concentrations in utero, maternal behavior, and offspring development, which re-creates (in pregnant female offspring) the initial hormonal conditions in the uterus. Genetically identical lineages can have different re-occurring phenotypes.
- Epigenetic persistence of cellular states, which depends on the operation of various autocatalytic mechanisms, also known as epigenetic inheritance systems (such as those involving the inheritance of methylation patterns, or three-dimensional protein structures). Such cellular variations are heritable, and there is growing evidence for the transmission of epigenetic variations not only in somatic cell lineages, but also through the germ line. Again, organisms with identical genotypes can have different and transmissible phenotypes.

As far as evolution is concerned, W-E believes that for evolutionary change to occur the transmissible variation must be genetic. She accepts Williams' distinction: "only the genetic inputs (to development) have been screened by selection. Selection may favor phenotypes that actively incorporate certain environmental elements, but it can only do this via gene frequency changes"

(p. 99). All other types of persistence are considered very important for development and selection, but not for evolutionary change, because they are deemed not to involve inheritance. I think that W-E reaches this conclusion for two reasons. First, because she does not make a systematic and clear distinction between the different types of persistence. Second, because of the fear that her views will be labeled Lamarckian, a label that may lead biologists to ignore them. However, although W-E's worry has a firm basis in the sociology of evolutionary biology, there is a price to pay: it leads to a lack of clarity and to an unnecessary and indeed harmful narrowing of her synthesis.

The inheritance of induced variations in phenotypes can be stable, and can lead to various evolutionary changes that do not involve changes in DNA base sequence. The attempt to ignore and trivialize such hereditary changes is unwarranted, and leads to mistaken interpretations not only of hereditary phenomena, but also of the relationship between genetic and non-genetic heredity and evolution (Jablonka et al. 1998, Jablonka and Lamb in press). It also leads to the neglect of the relationships between different types of environmental inputs. A persistent change in the internal environment is usually initiated by a change in the external environment. Sometimes there is absolute dependence on the persistence of the external environment, but this is not always the case. There is a spectrum of dependencies, and sometimes a change in the environment is a trigger for a long-lasting change that no longer depends on continuous induction. There are several recognized cellular and organismal mechanisms that stabilize the internal state and allow the internal environment to persist even when the inducing external environmental stimulus is no longer present. Furthermore, features of the social environment that are constructed by the activities of individuals can be perpetuated through social learning, leading via cultural evolution to local traditions in animals (Avital and Jablonka 2000). Selection among induced or learnt phenotypes that does not involve genetic change is then possible, and may lead to non-genetic cumulative evolutionary change.

Paradoxically, W-E's focus on the exclusive role of genes in evolutionary change, and her curious approach to genetic recombination, which she believes is unimportant as a source of adaptive phenotypic novelties (see, for example, p. 145), bring the gene-based view of evolutionary change back into the foreground. Although gene-combinations in sexually reproducing organisms are transient, and therefore cannot be the units of evolution, it is gene-combinations that underlay the expression of phenotypic traits that are selected. Single allelic variants, when considered in isolation are usually selectively neutral. As Waddington's experiments showed, and as W-E's own extensive discussion illustrates, most new phenotypic variations are the outcome of the activities of many genes with complex epistatic interactions. The stability of the phenotypic subunit that, as W-E rightly stresses, allows phenotypic recombination during evolution, is retained despite changes in alleles within gene-combinations, because there are internal mechanisms that lead to the stabilization of the expression of the phenotypic subunit during development and render the effects

of many allelic substitutions equivalent. Thus, in spite of her important focus on the primacy of the phenotype, and in spite of her equally important stress on the significance of phenotypic recombination in evolution, W-E does not treat phenotypic traits as units of evolution, and underplays the role of the internal mechanisms that lead to phenotypic persistence in spite of single gene variations.

### **Environmental modifications and genetic accommodation**

Although W-E stresses that both mutation and environmental induction can initiate a new phenotype, she advances convincing arguments for the greater evolutionary potential of environmental modifications. The major advantage of environmental induction is that it can be very persistent and can affect all (or most) members of a population, so it is unlikely to be eliminated in the way most new gene mutations are. In fact, because of this population-wide effect, an environmentally-induced modification can persist even if it is not initially beneficial. However, since by definition environmentally-induced modifications are correlated with the environment, and since they capitalize on pre-existing plasticity and on pre-existing regulatory organization that is condition-sensitive, they are more likely than gene mutations to be beneficial. Moreover, the population-wide effect of environmental induction means that unlike a new mutational effect, which initially occurs on a single genetic background, an induced environmental modification develops in organisms with many different genotypes. Hence, the chance that it will occur in a genetic background that leads to beneficial effects, and that therefore can be positively selected is substantially greater than that of a mutationally-induced modification.

Using this argument and the others I have discussed, W-E is able to extend the approach taken by Baldwin and Waddington, and to construct a much more comprehensive scheme, which includes not only the evolution of specializations but also the evolution of increased phenotypic flexibility. She provides an excellent and insightful analysis of the Baldwin effect and genetic assimilation, and diagnoses the many misinterpretations surrounding the concepts (including Waddington's misreading of Baldwin). Her belief that genetic accommodation, which includes but goes beyond genetic assimilation, is of central importance in evolution is founded on basic biological logic as well as a lot of circumstantial evidence. The lack of direct experimental evidence for genetic accommodation, which is a complaint likely to be heard from gene-centered biologists, is not surprising, because there are few long-term evolutionary processes that do have direct experimental support (a lot of evolutionary inferences are based on interpretations of comparative data). The prevalent emphasis on genes means that experiments designed to test the role of environmental induction in evolution are scarce. However, the circumstantial evidence is truly overwhelming: there is a vast amount of genetic variation, genetic and environmental effects are almost always interchangeable, and

environmental induction can lead to stable phenotypic effects that last for generations; genetic accommodation stabilizing the beneficial effects induced by new conditions and ameliorating deleterious side effects is highly likely, if not inevitable, in most such circumstances. The explanatory power of the concepts of phenotypic and genetic accommodation, and the many problems that they solve (in conjunction with her assumptions about the organization of phenotypes and the role of environmental induction) are masterfully explored throughout W-E's book.

In this review, I have concentrated mainly on the structure of W-E's argument, rather than attempting to review all aspects of the book. Each of the four parts really deserves a lengthy and detailed review of its own, and the last part, where the implications of her view for major evolutionary themes are examined, is particularly challenging. Although the book as a whole is a tour-de-force of data and ideas, it does suffer from some general problems. As W-E tells us in the preface, it was written over a very long period, almost rivaling Darwin's 20 years in writing the *Origin*. Although this enabled her to provide her readers with a wealth of data of encyclopedic dimensions, it is probably responsible for the many repetitions in the book, in which whole paragraphs are sometimes repeated almost word for word (for example, on p. 53 and p. 161). In addition, the legends to the figures are sometimes not explanatory enough for the general biologist, and a summary chapter is badly missing. Reading the book, I sometimes wished, for the sake of theoretical clarity, that W-E had been compelled to write an "abstract", like Darwin's *Origin*. Nevertheless, the book is a great achievement and provides the agenda for future research in evolutionary developmental biology, as well as a firm basis for a new and comprehensive post-synthesis synthesis.

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