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The Laws of Evolution and Derived Lawlike Principles

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The Laws of Evolution and Derived Lawlike Principles.—Sacha Haywood. 2007. Hagenia, Oxford. 493 pp. ISBN 97809 55740404. Hardcover, $57.—As much of the Western scientific community reflects on the Year of Darwin festivities, with all the self-congratulatory portrayals of the state of evolutionary theory and self-serving revisions of its history, *The Laws of Evolution* gives us pause. It reminds us that evolutionary biology owes its birth to an age-old desire to understand both the origin and the diversification of organismal forms, and that the first of these themes remains largely forgotten in the Darwinian theory of evolution. How and why such a central theme became marginalized over the past 150 years, while its erstwhile corollary—the principle of natural selection—was elevated to the level of the official dogma is a fascinating lesson in what happens to a scientific theory when it acquires an "ism" (as in Marx's theory of capital vs. Marxism and Darwin's theory of natural selection vs. Darwinism) and the reflection of a longing that we, biologists awed by the complexity of the world around us, have for a simple doctrine with near-universal explanatory powers.

That the two principles are necessary for realistic evolutionary explanations of biological diversity and complexity—the principle whereby developmental variation emerges and the principle whereby this variation is sorted and maintained—was recognized at least half a century before the publication of Charles Darwin's *Origin* (Darwin 1859). In fact, some of the major concepts that laid the foundation for Darwin's classic book—that species change over time and are related to each other by common descent, that evolution occurs through adaptation to the environment, that evolution proceeds both from simple to complex and the reverse (Darwin 1794, Lamarck 1809)—were driven by observations that the rules by which developmental variation emerges often seem distinct from the rules by which this variation is maintained and that both can influence historical change in a lineage. The enthusiasm with which Darwin's theory of natural selection was greeted by most of his contemporaries owes to its being viewed as a powerful complementary principle that would finally link the two well-established components of evolutionary theory—phenotypic variation that provides material for natural selection and inheritance of traits modified by selection that ensures evolutionary retention of favored configurations.

The conflict began when Darwin, while retaining the concept of Lamarckian inheritance intact, greatly marginalized the effect of developmental variation. Because very little was known about the rules of development or its actual mechanisms, there was no empirical basis for such dismissal other than Darwin's insistence on treating the principle of natural selection as the only creative force in evolution. For natural selection to be creative, developmental variation—the material for natural selection—would have to be "slight, random, and abundant." Such treatment of developmental and organismal variation, most evident in the first edition of *Origin*, prompted an outcry among some contemporary biologists, with objections ultimately crystallizing in Mivart's (1871) book—which Darwin called "the most serious threat" to his theory. By the sixth edition, Darwin somewhat softened his stance on additional forces in evolution, but the ensuing debate entangled the Darwinian theory of natural selection into a set of controversies that would continue to this day, resurfacing in such concepts as developmental constraints, incipient stages of trait functionality, the stasis of species, speciation burst, deep developmental homology, emergent variation, and punctuated equilibrium, each prompting a storm when questioning the exclusivity and primacy of natural selection in evolution.

In repeated attempts at mutualism between the two principles of evolution, the theory of development always ended up being consumed—the Darwinian school, often more Darwinian than Darwin himself, inevitably viewed development as a collection of past and present adaptations shaped by natural selection, while the Modern Synthesis confounded the rules of development with the rules of inheritance, giving us "inherited developmental toolkits." Haywood is correct in stating that the reason for such continuing failure is that we still lack a theory of development—a theory that defines the generative principles underlying the production of organisms. Devising such a rule—something general and universal enough to be called the law of development, on par with the law of natural selection—is the main goal of this ambitious book.

Haywood's view of development has roots in the late-19th-century embryological work that established that developmental processes proceed on the basis of successive inductions, each stage contingent on a previous one and directed by internal stimuli and inherited cellular templates. The induction stage is followed by the stage of competence, when the cells acquire the ability to respond to stimuli in a specific manner; the process concludes with the stage of determination, when a cell lineage commits to a particular developmental fate. The author calls induction, competence, and determination the most powerful concepts in biology and devotes much of the book to illustrating their strength and explanatory power in the formulation of the law of development. In turn, the developmental origin of evolutionary novelty is categorized into five lawlike principles underlying timing and pattern of expression, regulation, and construction of organismal structures. The categories of induction, competence, and determinism are

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then fitted into a truly bewildering array of natural phenomena—from behavioral imprinting, to sensitive periods of song learning, to variation in oogenesis, to electron orbits and the principles of quantum physics and biochemistry. For some biological phenomena, such fitting is very useful. Haywood makes a convincing case that an explicitly developmental consideration of the proximate mechanisms of avian clutch size greatly clarifies many questions that are difficult to answer from the ultimate perspective of natural selection acting on egg size and number.

In other phenomena the analogies seem to be taken too far and the category fitting seems forced; it is not obvious what exactly is clarified by characterization of reflexive behaviors and mental structures into induction, competence, and determinism or why the analogy between tissue–tissue interaction and behavioral responses is useful. The sentences that combine Newton, the Big Bang, Schrödinger, and Blue Tits are particularly breathtaking, but this is exactly the author's point—for the laws of biology to be laws, they have to apply to "everything from subatomic particles to galaxies or from gravitation to collision" and, most importantly, to the emergence and maintenance of complexity. Toward the end of the book, this thesis is taken to the extreme and the author occasionally leaves the confines of our planet and takes on the universe, comparing planets in the likely sequences of stages of emergence and the evolution of complexity. While the author is to be commended for taking to the logical extreme his call for the universality of laws of developmental variation and natural selection, some readers will find themselves wishing for greater scholarship. Essentially in a single breath and with scarcely any references to the original academic background, we are beamed through 19 major hypothetical transitions where the origin of life and the Big Bang are only small blips in the sequence of events. This perspective is so superficial that occasional errors (such as in the statements on the relative stability of different chemical compounds and the known sequence of events) seem wholly insignificant when one realizes the awesome scale of this cosmic journey. Afterward, an example of the versatility of different life constructs, illustrated by distinct anatomies of flight apparatus across metazoans, comes as a stunningly mundane bump on the flight through the universe that we just experienced. Returning to this planet, explanations of the phenomena by which natural systems show an orderly increase in complexity—something that the theory of natural selection does not explain well—are insightful. Here Haywood's solution is reminiscent of the one advanced by the proponents of emergence theory (Reid 2007) that states that a drive toward greater complexity is a byproduct of the constantly branching suites of traits generated by species' development as species struggle not to become extinct, such that complexity has no cause of its own and emerges despite natural selection, not because of it (Badyaev 2008).

Haywood is at his best in the first 12 chapters when expanding a fundamental premise that the maintenance of genetically determined characters in the population and its developmental origin are different things and that in order to bridge the gap between development and evolutionary theory we need to consider the extent to which "a regularity inherent in development and acting in concert with natural selection can share evolutionary paths." The first half of the book traces the historical origin of the concept of facultative variation, which states that development proceeds by largely autonomous and fitness-invariant steps with distributed internal and external controls and templates.

Haywood's historical account, although somewhat biased, nevertheless provides interesting insights into the personalities behind the greatest debates in evolutionary biology; we read correspondence of the famously "reluctant" Mr. Darwin actively sponsoring anonymous publications ridiculing the authors who challenged the exclusivity of his theory of natural selection, we learn of the origin of the time-honored tradition of painting the critics of the theory as populists and creationists, and we are fascinated by Darwin's persistence in distancing his theory from biological discoveries of the time that clearly provided a foundation for it, including the concept of natural selection advanced by Erasmus Darwin, his grandfather. All this contributes to a richer account of the history of evolutionary biology, especially valuable in light of its recent simplifications.

This large book really reads like two. The first exposes the limits of the current theory of evolution imposed by the theory of natural selection, and the second describes the laws of evolution. Whereas the first half is focused and well structured, the second half loses its focus and logic at times. The chapter on the mind–body dichotomy and the evolution of mental structures seems wholly out of place, and the prose, in places, gets repetitive and a bit pompous. Many pleas to "bear with me" highlight the need for better editing—which is especially unfortunate when poor editing gets in the way of understanding the concepts that the author describes. Missing also are essential discussions of the origin of inducible structures, the evolution and inheritance of competence, and the evolutionary stability of determination—all outstanding questions that preclude coherent incorporation of developmental biology in the theory of evolution.

The book opens simply and to the point: "This is a book about laws that govern the universe." The premise of such an extraordinarily tall order is that the true laws of evolution would account for the lawfulness existing in the cause of all things. Although the book does not succeed in meeting this goal—the law of development is never quite spelled out—it goes a long way in clarifying what, exactly, needs to be explained in evolutionary theory. Sometimes attempts at partial answers to important questions are far better than just criticism of the absence of answers.

As frustrating as this book may be at times, it can also be fascinating and stimulating. The overwhelming abundance of familiar bird examples will make many ornithologists take a fresh look at evolutionary theory and grant deeper insight into proposed concepts and principles. Plus, how often do you get to own a book on evolutionary theory with beautiful images of bird eggs on the front and back covers and four chapters devoted exclusively to insights into the evolution of avian clutch size, song learning, and food hoarding as proofs of lawlike concepts that also guide the universe.—Alexander V. Badyaev, *Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA. E-mail: abadyaev@email.arizona.edu.*

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