

## Preface

*Development* and *evolution* both, fundamentally, mean change, and both terms have long been applied to change in life. Over the nineteenth and twentieth centuries, these terms came to refer to quite different processes. Development is the process that an individual organism goes through over the course of its life, and evolution is the process that a population goes through as its members reproduce and die. August Weismann successfully argued for the conceptual separation of the germ line, which can evolve, from the soma, which can develop.

Advances in genetics produced the modern synthesis, which combined genetics and the theory of evolution by seeing evolution as a change in the genomes of a population over time. An early champion of this separation was G. C. Williams, and its current popular form is Dawkins's selfish gene. Dawkins (1976) argued that the gene is *the* unit of natural selection. On this view, natural selection looked through the organism right to the genome. Thus, the process of development was rendered epiphenominal to the process of evolution. The development of an organism with various traits was just a mechanism to differentiate the fitness of genes. Developmental biology continued to be studied, but, other than assuming various general ideas about adaptation, that study was largely segregated from the study of evolution. The conceptual separation of development and biology was widely seen as an important step in the rapid advance of biology in the twentieth century, because it allowed evolution to be studied without getting bogged down in the messy details of development.

This segregation has always had its dissenters, however. To see genes as the unit of natural selection misconstrues their role in evolution. Gould (2001, 2003) echoed an argument from Wimsatt (1980) when he said, "Units of selection must be actors within the guts of the mechanism, not items in the calculus of results." Gould went on to do other work that is beyond the view of the modern synthesis. He coined a new intellectual sin,

“adaptationism,” which involves seeing all traits as adaptations, rather than as the results of developmental constraints, and his view of punctuated equilibrium challenged the steady-as-she-goes, gene-by-gene sorting implied by the modern synthesis. Ironically, it was advances in genetics that lead to a greater interest the mechanisms of developmental genetics and their evolution, which brought development back into the fold. The remarkable conservation of developmental genes, such as Hox genes, cried out for an explanation that could only be given by considering both evolution and development.

There is now growing interest in the developmental synthesis (also known as *evo-devo*). Old ideas, such as *bauplan*, are being reviewed in a new light, and relatively new ideas, such as canalization, modularity, and evolvability, all essentially involving both evolution and development, are increasingly being incorporated into theoretical and empirical work. Evolutionary biologists are investigating developmental constraints and discovering how evolutionary transitions came about. A nice example of such work is Brylski and Hall's (1988a, 1988b) study on the evolution of external furry cheek pouches in *geomyoid* rodents. Pocket gophers and kangaroo rats store food in external cheek pouches. Developmental data showed that these pouches evolved from internal cheek pouches, which are not as adaptive because they are smaller and lose moisture to the food. Both types of cheek pouches develop from the buccal epithelium by epithelial evagination. Brylski and Hall discovered that the change to external pouches was due to a small change in location and magnitude of epithelial evagination at the corner of the mouth to include the lip epithelium. The corner of the mouth then became the opening to the external pouch as the lips and snout grew. That small change in the developmental mechanism produced a significant coordinated change in adult morphology, thereby contributing to the direction taken by evolution. In particular the developmental mechanism determined that the first external pouch was lined with fur (see Robert 2002 for further discussion of this and other examples of the developmental mechanisms of evolutionary novelty).

Widespread interest in the developmental synthesis is a relatively new phenomenon. It remains unclear just how much of a revision of evolutionary theory it requires (see Sterelny 2000 and Robert 2002 for opposing views). We hope that this book will act as a focus for this growing project. It is a relatively young project, and like so many young things, it is still unclear what it will be when it grows up. The more modest result of the new developmental synthesis is that developmental theory will supplement evolutionary theory. That is, theoretical and empirical work on devel-

opment will answer questions that have troubled evolutionary theorist or soon will. Almost certainly, the more modest project will be successful in some manner; work on development is bound to contribute to our understanding of evolution, because, after all, evolution is a process of the evolution of things that develop.

The more ambitious and more significant result of the developmental synthesis would be a fundamental theoretical rethinking of evolution itself. The developmental systems approach of Susan Oyama, Paul Griffiths, and Russell Gray (2001) is an example of this, although it seeks to integrate more than development into its reinterpretation of evolution. James Griesemer (2000) offers a purer developmental synthesis that hinges on what is distinctive to evolution and development (i.e., reproducers). The cases for these more extravagant developmental syntheses are still being made, and the jury is still out. All of the chapters in this book argue for the significance of evo-devo; some arguments are direct, but mostly the work here contributes to the synthesis itself. The success of these chapters would be a part of the success of the developmental synthesis.

In chapter 1, Manfred D. Laubichler and Jane Maienschein offer some historical vignettes to show how the study of biological generation separated into the study of development and biology in the late twentieth century; that there is indeed a growing interest in their reintegration; but this faces the difficulty that work in evo-devo is itself experiencing centrifugal tendencies. The most obvious is that some integrate development and evolution by using information about evolution to learn about developmental mechanisms, while others use information about developmental mechanisms to learn about evolution. This could be the result of the previous division between developmental and evolutionary biology as each camp continues to be biased in the questions that they want to answer. Laubichler and Maienschein suggest that recent history shows there is the will and even possibly some funding to bridge these two cultures and truly balance an interdisciplinary field. However, they warn that the history of evo-devo (as described above) may ultimately be judged as a naive myth, unless a unifying set of theoretical principles for evo-devo are established. A new genuine synthesis may remain elusive, due to a lack of experimental success and theoretical structure.

Werner Callebaut, Gerd B. Müller, and Stuart A. Newman's organismic systems approach to biology—described in chapter 2—offers one set of unifying principles. Their view is founded on emphasizing causation over correlation. They see development as the causal mechanism for the process of evolution. This turns evolution on its head. Rather than evolution

producing organisms that develop, “Development has resulted in populations of organisms that evolve.” They too investigate the potential for evo-devo to change evolutionary theory, and like Laubichler and Maienschein, investigate the forces that integrate and disintegrate science in general and evo-devo in particular.

The modern synthesis ignored how genotype determines phenotype, which was left to be studied by developmental biologists. In chapter 3, H. Frederik Nijhout offers a mathematical model for representing the genotype-phenotype relationship in an  $n$ -dimensional hyperspace. The model is based on plausible developmental assumptions. Combinations of trait values determine phenotypes, allowing all possible phenotypes to be represented. By considering changes in just one gene on one aspect of a phenotype, we can see how that gene influences that phenotype. By considering variations in other genes, too, we can see how the way the first gene influences that phenotype can change. That is, other genes determine the developmental program, which may be understood as providing constraints. One novel result of this is a distinction between evolution that occurs within the constraints of a given set of developmental mechanisms, versus evolution that results from changes in developmental mechanisms. This concrete representation of constraints coming from a developmental biologist provides one promising way that abstract concepts of evo-devo may be empirically studied and quantified in order to produce specific predictions.

As chapter 4 suggests, Gerhard Schlosser builds his integrated view of development and evolution around a broader notion of constraints than is usually considered in evolutionary biology. For him, constraints arise from the necessity to maintain a stable/functional organization after variation. Changing one trait will tend to require changing some other traits, but not all others. Significantly, this includes not only generative dependencies typically thought of as determining constraints, but functional dependencies that are necessary for organism viability too. Mutually constraining factors bundle together to form the units of evolution. Because these units of evolution can correspond to modules of development or behavior, results from physiology can play an important role in their discovery.

In chapter 5, Roger Sansom argues for the general adaptive value of gradual mutation and that this can only be selected at a multigenerational level. Therefore, there is another unit of selection—a legacy. Because generative entrenchment is a generic feature of complex organisms, he suggests that this selection will encourage developmental modules that are functionally integrated. The nontriviality of this thesis requires that the identities of

functions are not determined by physiology. Instead, Sansom looks to ecology for an answer.

Paul E. Griffiths largely assumes that evolutionary developmental biology has been productive for the study of evolution and, in chapter 6, applies its lessons to psychology. Recent work in evolutionary psychology has assumed the modularity of the brain. However, Griffiths argues that this work is suspect because it has failed to take account of homology as an organizing principle as well as the ecology of psychological development. The evolutionary developmental ecological psychology Griffiths endorses is not unlike the classical ethology that was eclipsed by sociobiology in the 1960s. This completes an intellectual circle, because it was this sociobiology that inspired Gould's attack on adaptationism, which was an important step toward the current interest in the developmental synthesis.

In chapter 7, William C. Wimsatt and James R. Griesemer attempt to get a handle on identifying the units in cultural evolution by applying the notion of development. They make use of the notion of scaffolding in cultural evolution—the idea that permanent or recurring social and material structures are important to inheritance in culture. Incorporating one of the earliest ideas in evo-devo, Wimsatt's "generative entrenchment" and Griesemer's more recent "material transfer," they begin the work of characterizing the dynamic interplay between channels of inheritance to identify the units of cultural change. Incorporating development is of particular importance to understanding cultural evolution, because many enthusiasts have become enthralled by Dawkins's idea of a cultural meme (a replicating unit analogous to a gene in biological evolution). The search for memes is a search that has been blind to what would count as development in culture and the insight that incorporating development might bring. However, the complexity of cultural evolution results in memetics having less to offer than gene selectionism and, as the developmental synthesis does in general, Wimsatt and Griesemer attempt to investigate the complexities of cultural evolution, rather than abstracting them away.

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