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Introduction: Evolutionary Developmental Mechanisms

This book deals with mechanisms of evolutionary change, especially those mechanisms involving embryonic development as the vehicle for evolutionary change. The field that embraces such studies is known as *evolutionary developmental biology* or *evo-devo*. Evo-devo forges a synthesis of those processes operating during ontogeny with those operating between generations (during phylogeny). Evo-devo includes, but is not limited to:

Analyses of how embryonic development arose and evolved
The role of embryonic development and developmental processes in the evolutionary modification of existing features and in the origin of new (often novel) features
The origin, modification, suppression, or loss of life history stages
How genotype and phenotype interact over generational and gestational time spans
How development and ecology interact and co-evolve

The range of topics in this book reflects both the breadth of evolutionary developmental biology and the increasingly important role this discipline is playing in modern evolutionary and developmental biology. By development we mean any and all stages of an organism's life cycle from egg to embryo, to larval stage (in those animals with indirect development and, consequently, with metamorphosis), to newly emerged (hatched, born) offspring, through to adulthood, cessation of growth, and senescence.

Development occupies the all-important middle ground between the genotype and the phenotype. Although developmental processes figure prominently both in the production and evolution of the phenotype, and in the origin of novelties and new species, the role of development in evolution is too often neglected. The issue is not that we do not under-

stand developmental processes; we have an extraordinary knowledge of how development works. For example, we have an extensive understanding of how genes function, both in individuals and in populations. We can describe the features (structures, behaviors, life history stages) that comprise the phenotype, and we realize that the phenotype is not a one-to-one readout of the genotype. It is no longer a question of whether ontogeny recapitulates (Haeckel) or creates (Garstang) phylogeny; we now appreciate that relationships between ontogeny and phylogeny are in fact reciprocal. Ontogeny enables phylogenetic change; ontogeny also evolves, and evolutionary change can take place at all stages of development.

We are just beginning to understand the evolutionary and developmental processes that constitute what we call *evolutionary developmental mechanisms,* which are the processes of development that mediate descent, whether that descent involves modification or stasis. Our aim in producing this book is to present those mechanisms and approaches in a way that illustrates the current state of the discipline and illuminates the road ahead for evo-devo—indeed, we believe, the road ahead for biology as an integrated and integrative discipline. To that end, the book discusses concepts and approaches at multiple levels of biological organization.

Natural selection operates at any of the hierarchical levels of individuals, kin, or groups, and on genes, gametes, zygotes, cells, or populations. Although often regarded as the raw material of evolution, genes do not make structures; there is no direct, one-to-one relationship between genotype and phenotype. Genes exert their influence on evolutionary change through mutations, duplications, rearrangements, novel cascades and networks, conserved patterns of expression, and so forth. The types and mechanisms of mutations are many and varied, including nucleotide substitutions, point mutations, insertion of transposable elements, shuffling of exons, and inversions of chromosomes. Some mutations are neutral but many are potentially beneficial. All are subject to selection, either directly or indirectly. Similarly, phenotypes and the processes that produce them are subject to selection; cells, embryos, and modifications of genetic and developmental processes are as much the raw material of evolution as are genes and mutations.

Evolutionary developmental mechanisms exist as a hierarchy of processes and so can be studied at all structural levels from genes to populations, using the wide variety of techniques and approaches developed in

other fields. This diversity of mechanism and approach is both a strength and a drawback. On the one hand, a multitude of mechanisms act either alone or synergistically to effect evolutionary change. On the other hand, understanding and synthesizing this diversity demands a truly integrative approach and increased communication among the traditionally separate fields of genetics, molecular biology, developmental biology, paleontology, phylogenetics, morphology, and ecology (to name a few). No unified theory of evo-devo exists. However, many of us assume that development will find a more inclusive place in the study of evolutionary biology, just as it will find a more central role in studies of life history strategies, phenotypic plasticity, and ecological communities, to name a few.

To move toward these goals, we have invited experts with a diversity of backgrounds to contribute to this volume. Arranged alphabetically, the entries exemplify the hierarchical approach that is so characteristic of evo-devo and that is required to understand, in their fullness, developmental, evolutionary, and evolutionary developmental processes.

Topics traditionally associated with the Modern Synthesis, such as evolution, genetics, environment, selection, speciation, phylogenesis, variation, evolvability, and the relationship between the phenotype and genotype, occupy a central position in evo-devo, and so are included in this volume. Also included are discussions at the level of the gene, including regulation, cascades, and gene-gene interactions. At the cellular level, central topics such as cell division, determination, differentiation, patterning, interactions, and the role of cells in embryonic inductions are discussed in the context of their roles as evolutionary developmental mechanisms. Entries on genome size, epigenetic processes, and genomic and extragenomic inheritance show how genetic and cellular levels are linked.

The links among cells, tissues, and organs are discussed in such contexts as modularity, segmentation, epithelial-mesenchymal interactions, patterning, complexity, growth, heterochrony, and heterotopy. Links between development and morphology at the organismal level are discussed in the context of morphogenesis, ontogenetic repatterning, canalization, genetic assimilation, and structural and functional accommodation. Changes in life history are treated with reference to innovations and novelties, life history evolution, larvae, constraints, plasticity, and polymorphism.

The authors were encouraged to present and develop their own per-

spectives on their topics. Each provides an overview of the current status, the central concepts and approaches of evo-devo, and where the field is moving. Some entries include historical or philosophical background. We are delighted that John Bonner accepted our invitation to write the foreword. His seminal studies, which span half a century, laid the foundations for the current field of evo-devo.

How to Use This Book

The entries are arranged alphabetically by subject. Gilbert and Burian's entry, "Development, Evolution, and Evolutionary Developmental Biology," may be a good place to begin. This entry provides an overview of evo-devo and places the field in a historical context.

We placed references for all entries in a single bibliography at the end of the volume. The comprehensive index also serves as a glossary. To find definitions of terms, concepts, or ideas, consult this index. We also used the index for cross-referencing between entries. Genetic nomenclature follows Appendix 1 in Wilkins (2002).

Although we believe that we have covered the major concepts and approaches in evo-devo, we welcome your comments.

Keywords and Concepts in Evolutionary Developmental Biology