Understanding Development

Developmental biology is seemingly well understood, with development widely accepted as being a series of programmed changes through which an egg turns into an adult organism, or a seed matures into a plant. However, the picture is much more complex than that: is it all genetically controlled or does environment have an influence? Is the final adult stage the target of development and everything else just a build-up to that point? Are developmental strategies the same in plants as in animals? How do we consider development in single-celled organisms? In this concise, engaging volume, Alessandro Minelli, a leading developmental biologist, addresses these key questions. Using familiar examples and easy-to-follow arguments, he offers fresh alternatives to a number of preconceptions and stereotypes, awakening the reader to the disparity of developmental phenomena across all main branches of the tree of life.

Alessandro Minelli is a former professor of zoology and, in retirement, a senior scientist at the University of Padova, Italy. He is an honorary fellow of the Royal Entomological Society and the Italian Society for Developmental and Cell Biology. He is the author of numerous books on evolutionary and developmental biology, including *The Development of Animal Form* (Cambridge, 2003), *Plant Evolutionary Developmental Biology* (Cambridge, 2018) and *The Biology of Reproduction* (Cambridge, 2019; with Giuseppe Fusco).

The ***Understanding Life*** series is for anyone wanting an engaging and concise way into a key biological topic. Offering a multidisciplinary perspective, these accessible guides address common misconceptions and misunderstandings in a thoughtful way to help stimulate debate and encourage a more in-depth understanding. Written by leading thinkers in each field, these books are for anyone wanting an expert overview that will enable clearer thinking on each topic.

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'This is the finest book on the principles underpinning biological development that I have read in a long time. It is succinct, thoughtful and full of examples, offering wise reflection on the diversity of developmental phenomena across the whole tree of life. Understanding Development is especially notable for its organization into 48 sections comprising 8 chapters. Each section subtitle states a key lesson to be learned through brief historical and theoretical expositions, well-chosen examples, and stories of odd-ball and familiar life forms. Every lesson overturns some conventional wisdom or common knowledge that cannot stand up to the wondrous diversity of life on Earth. Minelli's broad, deep knowledge of the field is expressed with an engaging contrarian spirit that serves his larger goal: to prompt a reassessment of the state of contemporary understanding of development in a way accessible to novice and expert alike.'

James Griesemer, University of California–Davis, USA

'Developmental biology has been described as the process by which a fertilized egg is transformed into a multicellular organism. But is it? In this thoughtful and erudite book, Alessandro Minelli forces us to step back and reconsider the subject. Using an astonishing range of examples, from pythons to lichens and from sponges to ciliates, Minelli challenges a series of generalizations and preconceptions. We see how development is not only the process of building adults, why development does not have end-points, how development need not start with a fertilized egg, why we must be careful with the concept of developmental genes, and much more. After reading this book, you might not think about developmental biology in the same way again.'

Peter Holland, University of Oxford, UK

'Developmental biology is a highly dynamic area of the life sciences, and it also lacks a unifying theoretical framework and must rely on general principles derived from a small number of well-studied model organisms. In Understanding Development, Minelli channels an encyclopaedic knowledge of biological diversity to show convincingly the need for a more expansive concept of development that can embrace the variability and complexity of life. Minelli surveys the interplay of generalizations and exceptions that arise in the study of development, tracing out important open conceptual challenges facing researchers today. Engagingly written and always insightful, this book is highly recommended to biologists, philosophers of biology, and historians interested in grappling with a fundamental and active problem area in the contemporary landscape of biological thought.'

James DiFrisco, KU Leuven, Belgium

To the inspiring disparity of Life

Contents

Foreword

Alessandro Minelli has written an exceptionally rich book with great insights. *Understanding Development* shows that in contrast to our adult-centric and anthropocentric view of development, there is a variety of developmental processes in nature. The author effectively debunks numerous misunderstandings about development, some of which you may never have thought of before. The whole book is structured in such a way that all misunderstandings are explicitly discussed and addressed one after the other. In doing so, the author provides exceptionally clear examples from a variety of organisms, which clearly show the complexities of developmental processes and his exceptional knowledge of the topic. Minelli takes readers on a delightful and informative voyage across all forms of life and shows that development can be quite different from what we know from our own experience. He effectively makes the case that to understand life we need to look at other forms of life and their developmental processes. The present book is a fantastic means for doing this; once you have read it, you will feel stunned by the unity and diversity of life that are presented throughout.

Kostas Kampourakis, Series Editor

Preface

For centuries, the study of development was strictly descriptive, and the main tool available to the researcher was the microscope.

At the beginning of the nineteenth century, this discipline witnessed one of its greatest successes: the discovery of the mammalian egg by Karl Ernst von Baer. Shortly thereafter, the cell theory enunciated by Theodor Schwann in 1839 consolidated life sciences by recognizing a similar organization in animals and plants: cells, the structural elements of which multicellular organisms are made, are also the building blocks of development.

Experimental embryology emerged towards the end of the century. Observation was now complemented by mechanical manipulation and by exposure of eggs and embryos to a diversity of chemicals. The resulting discoveries impinged strongly on the interpretation of developmental phenomena. However, the comparative spirit that had hitherto pushed embryologists to conduct their research on a sample of species as numerous and varied as possible began to vanish. Biological research now focused increasingly on a few model species – from Gregor Mendel's peas to Thomas H. Morgan's fruit flies, from Wilhelm Roux's frogs to Hans Driesch's sea urchins, from Theodor Boveri's large roundworms to Hans Spemann's newts.

The naturalistic season of developmental biology seemed to be definitely over, except for its solid legacy in the notion of development as the story of the changes that transform an egg into an adult animal, or a seed into a mature tree.

In the meantime, advances in cell biology fuelled increasingly successful studies of the mechanisms responsible for these changes, from cell

proliferation to growth to differentiation. Some of these processes are seemingly common to all organisms, at least to multicellular organisms; others are more specific, for example to plants or to animals only, or even to smaller groups, but it seems reasonable to ignore the minor differences that may exist between one species and another, and instead to emphasize patterns and mechanisms shared by the widest range of organisms. These results became the increasingly solid corpus of general biology.

A decisive turning point was dictated by the entry into the molecular era. The study of genes was no longer limited to the rules of transmission from one generation to the next, but opened up to the investigation of where and when genes are expressed (that is, transcribed into messenger RNA molecules and eventually translated into proteins) during development, and how their expression is regulated. It did not take long to discover that many processes depend on the expression of the same genes in animals as diverse as mice and fruit flies. The temptation to extrapolate general principles from experiments restricted to a few model species was stronger than ever. But before long, many researchers realized that the taxonomic sampling of the living world must be widened again.

From time to time, biologists (and philosophers of biology) feel the need to revisit the basic principles of developmental biology, but this discipline turns out to have only a modest and uncertain body of theory, especially if compared to evolutionary biology.

One might expect that the list of contentious conceptual issues in developmental biology would shrink with the continuous progress of experimental research but, on the contrary, this list becomes longer and longer. Many of these critical issues must be left in the hands of skilled professionals; others, however, are based on traditional misconceptions that can be addressed here.

There are many excellent books, both popular and academic, that describe the stages of embryonic development of animals, the expression of genes involved in patterning a flower or the trunk of a fly, the molecular dialogues between the cells, or the intricate regulatory networks whose protagonists are the genes and their products.

This book is different: it is full of stories involving quite a number of different plants and animals, fungi and protists (single-celled organisms). The track will

not be dictated by taxonomic subdivision, but by the problems to be faced to lighten our vision of development from a long list of preconceptions and unjustified generalizations, unfortunately shared by a number of professionals.

Life is a product of history. This cannot be ignored in the fields of developmental and evolutionary biology, the scope of which is the study of change. Therefore, developmental biology cannot omit a systematic exploration of the many different forms in which development takes place in the different groups of living beings.

In Chapter 1, in addition to providing a historical framework, I discuss a possible definition of development and the need to abandon the finalism still latent in developmental biology today. In later chapters I discuss cells (Chapter 2), embryos (Chapter 4), developmental sequences (Chapter 5) and genes (Chapter 6). I do this not to summarize the notions that modern textbooks present with all the necessary technical detail, but rather to address, at each level, the most serious generalizations. The remaining chapters are dedicated to aspects that, in different ways, also affect the philosophy of biology. I discuss here individuals (Chapter 3), regularity of form (Chapter 7) and developmental ecology, with several pages dedicated to temporal aspects such as age, senescence, and the articulation of individual development into a sequence of steps (Chapter 8).

In 1802, Treviranus and Lamarck introduced, independently, the name 'biology' for the science of living beings. More than 200 years later, the time seems to have come to approach biology as the science of all life forms and to avoid reducing it to abstract generalizations.

In the following pages there are rather more stories about animals than about plants, fungi and other kinds of organisms. In part, this is justified by the amazing wealth and complexity of developmental patterns and processes exhibited by animals; in part it is the consequence of my professional rooting in zoological disciplines. This bias notwithstanding, I hope that the reader will share my fascination with the inspiring disparity of developmental mechanisms behind the 'endless forms most beautiful' that evolved along all branches of the tree of life.

Acknowledgements

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