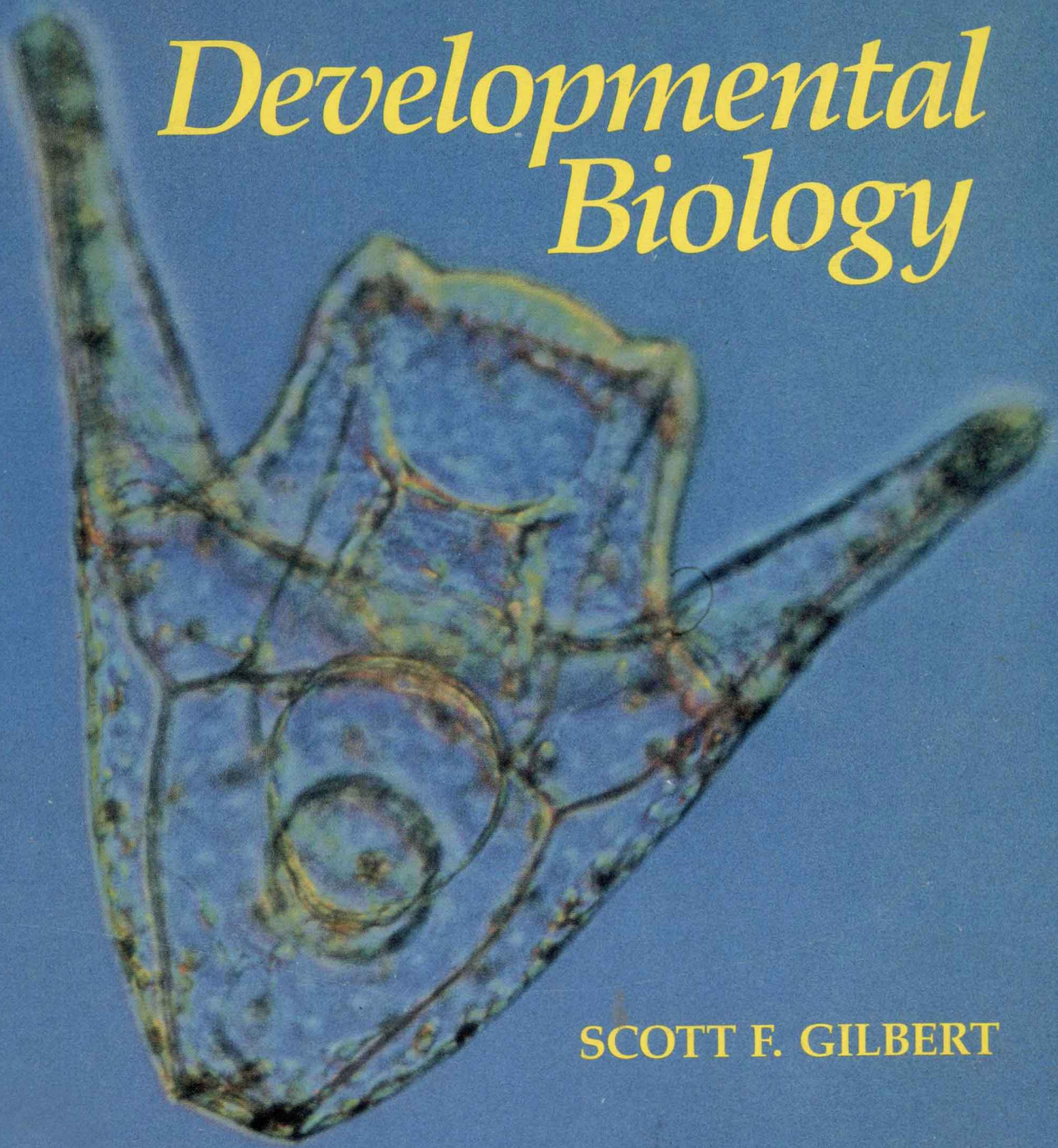
Developmental Biology



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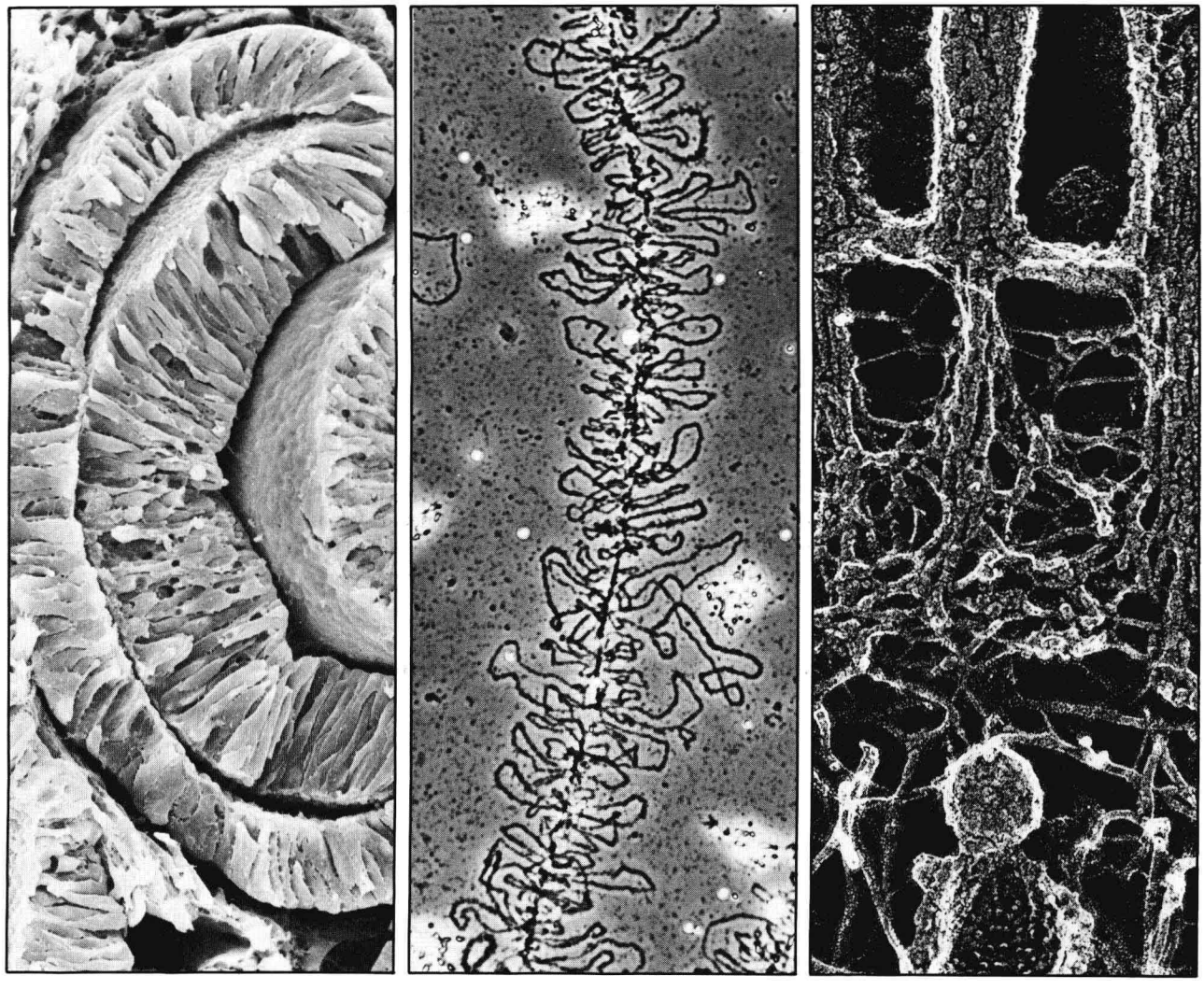

To Daniel and Sarah

THE COVER
Pluteus larva (front cover) and 32-cell stage (back cover) of the sea urchin *Lytechinus pictus*. Courtesy of George Watchmaker, Lawrence Livermore National Laboratory, Livermore, California.

DEVELOPMENTAL BIOLOGY

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PREFACE

If there is anyone more foolish than the student who thinks he or she can learn all developmental biology in one semester, it is the professor who believes he or she can teach it. How much more foolish, then, is the person who writes a book for them? The motivation for writing this volume was the challenge to put recent advances in developmental biology into a coherent historical and conceptual order. This is not the only order possible. One of the strengths of contemporary developmental biology is that it attracts people from diverse backgrounds and training. Every developmental biologist has a preferred way of integrating the hypotheses and observations concerning animal development, and there is no one "best" way to introduce students to the field. Similarly, there is no one best way to write a textbook, and I feel that I should outline my basic principles at the outset.

First, this is a textbook written with juniors and seniors in mind. It does not assume a level of biology more sophisticated than that given by most good introductory biology textbooks, but a familiarity with cell biology and genetics will certainly make the going easier.

Second, the book is divided into three sections. The first section analyzes the basic phenomena and patterns of animal development from fertilization through the formation of the major embryonic organs. This section is placed first to provide the context for the more molecularly-oriented chapters that follow. This allows the analyses of differential gene activity and cell interactions to be placed within the framework of microscopically observable development. The second section focuses on the mechanisms of cell determination and differentiation, discussing the ways by which cells of an embryo become different from one another and from their progenitors. The third section concentrates on the other major problem of development—morphogenesis, the processes by which cells interact to form highly complex tissues and organs.

I have also tried to order the chapters in a manner that allows the student to have a conceptual framework in which to understand each successive chapter. Thus, the order of certain chapters differs from what might be expected. This is most obvious in that this book begins with fertilization and ends with gametogenesis. Here, the fertilization chapter includes a large section on the structure of the gametes, while the details of gametogenesis are saved until the end of the book, where the intricate gene activities and cell-cell interactions can be appreciated. (Thus, one can discuss the expression of vitellogenin genes and the

interactions of the oocyte and follicle cells after first having a general understanding of the translational control of gene expression and the importance of gap junctions.) Putting gametogenesis last not only allows it to be used as a culminating example of development but also provides a circular return to the beginning.

Third, this book is organized by principles, not by "systems." This allows one to see the major themes and variations of animal development. In the chapter on cleavage, the earliest developmental stages of various different organisms are contrasted and compared, while in the chapter on translational control of gene expression, the regulation of oocyte messages, globin messages, and casein messages are discussed together. So, while there is no one chapter on insect development, such information can be found in nearly every chapter of the book. Similarly, there are no chapters entitled "History of Embryology" or "Development of the Immune System." Having worked in these fields, I have too much respect for them to confine them to isolated (and often unassigned) chapters. I have introduced these topics, throughout the book, within their appropriate contexts.

Fourth, the text attempts to present developmental biology as a dynamic human endeavor based on repeated observations and controlled experiments. Since the data herein do not exist independently of the people who obtained them, I have included numerous citations so that interested individuals can read the original publications.

Fifth, I have tried to respect both the organismal and the molecular approaches to development, integrating them in various degrees in each section. I believe that the integration of molecular, cellular, and organismal approaches, if successful, should provide a richer understanding of development than any of these approaches taken individually.

Sixth, this book attempts to blur some of the lines separating developmental biology, genetics, and evolution. I have emphasized the use of genetic mutants to analyze normal developmental processes and have tried to show that some of the most intricate events on the molecular level are responsible for enabling the developing organism to survive in a particular environment. Moreover, when we say that one species has evolved into another, what we mean is that its development has changed. Genetic mutations affect evolution by working through development, and the elucidation of the mechanisms by which this is accomplished promises to be one of the most exciting chapters of modern biology.

Seventh, I have tried to increase the flexibility of this book by including "Sidelights and Speculations" sections. Their roles are twofold. Some take a concept introduced in the text and relate it to another field of biology. Others explore concepts which are too new or controversial to be included in the main body of the book, but which may be very exciting areas in the next few years. These latter sections are my attempts to keep the book from being rapidly outdated in such a quickly moving field.

Acknowledgments

The creation of a textbook is not unlike the creation of a complex organ or organism. During its four-year gestation, this book has developed in ways barely hinted at in the first drafts. As in organ formation, the interactions enabling these developments can be roughly divided into permissive ones and instructive ones. Those individuals having instructive interactions with the text (that is, where the information herein would be different, had they not intervened) include R. Auerbach, G. Florant, R. Freter, R. Herlands, J. Jenkins, J. Lilien, A. Mahowald, R. Marchase, M. Oster-Granite, S. Roth, R. Savage, B. Shur, and D. Sonneborn. D. Kirk, J. Gerhart, L. Iten, R. Raff, and the late R. Briggs have been especially helpful in forming the current state of this book. The readability of this text has been greatly improved by comments of students in my developmental biology and developmental genetics courses, and a large debt of gratitude (by all those who are assigned its chapters) should go to them and especially to my teaching assistants, L. Klein, R. Nelson, W. Kirby, D. Sivitz, and T. Kushner. Since my own views of development and how to teach it have come in good measure from certain excellent teachers and advisers, I wish to acknowledge their continued presence in this book.

But instructive interactions alone neither an organ nor a book make. The entire project would have come to a halt were it not for the numerous scientists who sent me their photographs and the extremely supportive biology department of Swarthmore College. H. Ewing and G. Flickinger must be singled out for working beyond the call of duty when I needed immediate typing or photographic development. The continuous updating of these chapters has been made possible by the computer wizardry of two students, B. Datloff and R. Mahajan, who felt that the best way to do well in my course was to type the text used in it. From the conception of this book through its delivery, Andy Sinauer and his staff have gently and effectively assured its proper development. My special thanks to C. Wigg and J. Simpson for their editing and to L. Meszoly, J. Vesely, and J. Woolsey for their art and production work on the book. Moreover, this book would never have been completed were it not for the encouragement of my wife, Anne Raunio, who, as an obstetrician, knows the joys of developmental biology and who felt that I should go through the experience of labor, if only with a book. My thanks to them all.

SCOTT F. GILBERT

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PART II: MECHANISMS OF CELLULAR DIFFERENTIATION

PART I

Patterns of development

CHAPTER 1

An introduction to animal development

It now remains to speak of animals and their nature. So far as we can, we will not exclude any one of them, no matter how mean; for though there are animals which have no attraction for the senses, yet for the eye of science, for the student who is naturally of a philosophic spirit and who can discern the causes of things, nature which fashioned them provides joys that cannot be measured.

—ARISTOTLE (CA. 330 B.C.)

Joy in looking and understanding is nature's most beautiful gift.

—ALBERT EINSTEIN (1953)

Introduction

According to Aristotle, the first embryologist known to history, science begins with wonder. "It is owing to wonder that people began to philosophize, and wonder remains the beginning of knowledge." The development of animals has been a source of wonder throughout human history, and it has constantly stimulated individuals to seek the causes for such remarkable, yet commonplace, phenomena. The simple procedure of cracking open a chick egg on each day of its 3-week development period provides a remarkable experience—a thin band of cells is seen to give rise to an entire bird. Aristotle performed this experiment and noted the formation of the major organs. Most any person can wonder at this phenomenon, but it is the scientist who seeks to discover how development actually occurs. Rather than dissipating wonder, our new understanding increases it.

Multicellular organisms on earth do not spring forth fully formed. Rather, they arise by a relatively slow process of progressive change that we call DEVELOPMENT. In nearly all cases, the development of a multicellular organism begins with a single cell—the fertilized egg, or ZYGOTE—which divides mitotically to produce all the cells of the body. The study of animal development has traditionally been called EMBRYOLOGY, referring to the fact that between the stage of the fertilized egg and birth, the developing organism is known as an EMBRYO. However, development does not stop at birth—or even at adulthood. Most organisms never cease developing. Each day, we replace over a gram of skin cells (the older cells being sloughed off as we walk), and our bone marrow sustains the development of millions of new erythrocytes every minute of our lives. Therefore, in recent years, it has become customary to speak of DEVELOPMENTAL BIOLOGY as the discipline that involves studies of embryonic and other developmental processes.

Developmental biology is one of the most exciting and fast-growing fields of biology. Part of its excitement comes from its subject matter, for we are just beginning to understand the molecular mechanisms of animal development. Another part of the excitement comes from the unifying role that developmental biology is beginning to assume in the biological sciences. Developmental biology is creating a framework that integrates molecular biology, physiology, cell biology, anatomy, cancer research, immunology, and even evolutionary and ecological studies. The study of development has become essential for understanding any other area of biology.

Principal features of development

Development accomplishes two major functions. It generates the cellular diversity and order within each generation, and it assures the