

Developmental Biology

NINTH EDITION

SCOTT F. GILBERT

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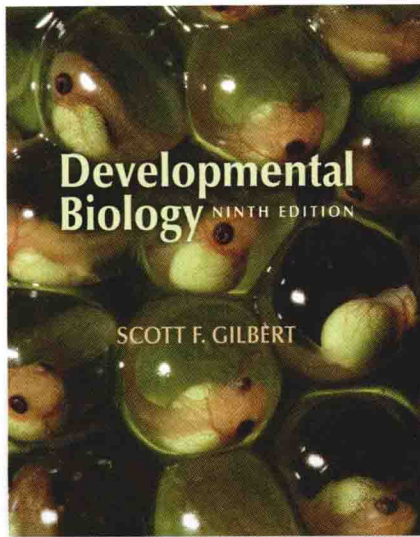
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The Cover

Three-day-old embryos of Costa Rican red-eyed tree frogs (*Agalychnis callidryas*). The female frog lays her eggs on a leaf overhanging a pond, so that when the tadpoles hatch (normally in about 7 days), they wiggle out and fall into the pond. The tadpoles' development is exquisitely tuned to their environment, and the larvae place their branching gills near the oxygen-rich egg surface. Tadpoles respond rapidly to the presence of infectious fungi or predaceous snakes, hatching early (often at 5 days) and taking their chances in the pond rather than succumbing to predation (see Chapter 18). Photograph courtesy of Karen Warkentin, Boston University.

Developmental Biology, 9th Edition

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DEVELOPMENTAL BIOLOGY

NINTH EDITION

Companion Website

www.devbio.com

devbio.com is an extensive Web companion to the textbook that is intended to supplement and enrich courses in developmental biology. Here you will find additional information for advanced students as well as historical, philosophical, and ethical perspectives on issues in developmental biology. Included are articles, movies, interviews, opinions (labeled as such), Web links, updates, and more. (There is even a developmental biology humor page!)

The site is comprised of Web topics relevant to all areas of the textbook, organized by textbook chapter. These topics are referenced throughout the textbook, both within the chapter, and at the end of the chapter. From the home page of the site, you can browse by chapter, search all topics, or quickly jump directly to any specific topic. The site also includes the complete Literature Cited for the textbook, most with links to the PubMed database.

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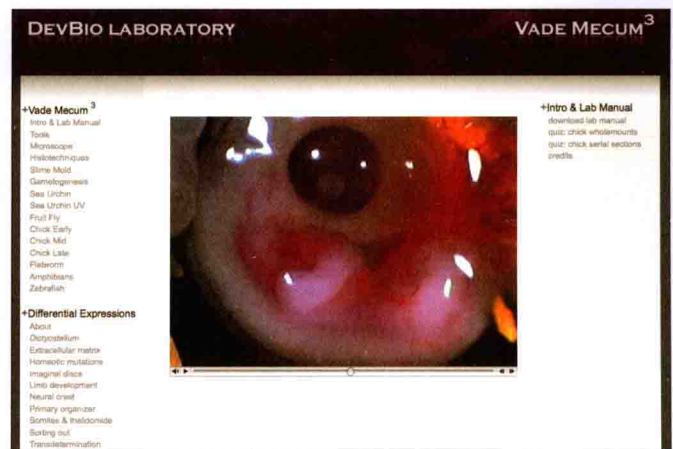
An Interactive Guide to Developmental Biology

Mary S. Tyler and Ronald N. Kozlowski

<http://labs.devbio.com>

Designed to complement the textbook, this unique resource helps you understand the organisms discussed in lecture and prepares you for the laboratory. **DevBio Laboratory: *vade mecum*³** is available online, which allows you the flexibility to use the software from any computer with Internet access. Access to the site is included with each new textbook.

Over 140 interactive videos and 300 labeled photographs take you through the life cycles of model organisms used in developmental biology laboratories. The easy-to-use videos provide you with the concepts, vocabulary, and motivation to enter the laboratory fully prepared. A chapter on zebrafish addresses how to raise the organism and the effects of various teratogens on embryonic development. The site also includes chapters on: the slime mold *Dictyostelium discoideum*; planarian; sea urchin; the fruit fly *Drosophila melanogaster*; chick; and amphibian.



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About the Book

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Developmental Biology

NINTH EDITION

To Daniel, Sarah, and David

Preface

It has become increasingly embarrassing for me to ask students to read the Eighth Edition of this textbook. It's so, well, 2006. Developmental biology has progressed so rapidly in the past four years that my lectures have fundamentally diverged from their reading. My "big" lecture on transcription now focuses on the ability of transcription factors to reprogram cell fates; and my lectures on stem cells and cloning have scrapped the notion of therapeutic cloning altogether, focusing instead on induced pluripotent stem cells. In both instances, we discuss what this means for understanding normal development, as well as what implications these technologies have for the future of medicine. Neither induced pluripotential stem cells nor "transdifferentiation" was established when the last edition of this book was published.

Even my most basic lectures have changed. The lecture on fertilization has to cover the new data on mammalian egg activation. My lectures on sea urchin development—an area of study that has been fundamental to developmental biology for over a century—now include systems theory operations involving double-negative gates and feedforward loops, and my evo-devo talks have led to discussions of mathematical modeling and parasitism. I can't talk about limb development without including the variations seen in dachshunds and bats, and I can't discuss sex determination without using the β -catenin model for mammalian ovary production. None of these areas were covered in earlier editions of my book. So this is really a very new edition. My editor tells me it has close to 700 new references; she only wishes I had deleted at least that many old ones.

Developmental biology is in a state of rapid metamorphosis. And, as in insect and amphibian metamorphosis, some old tissues remain the same, some get substantially remodeled, and some old tissues perish altogether; and all the while, new tissues are forming new structures. I hope that I have gotten these correct, and that the added new material will stand the test of time. I have tried to remodel the retained material into new narratives that are more inclusive of the data, and to appropriately jettison the information that was needed for earlier stages of the book's development but which is no longer needed by undergraduates.

Embryologist John Fallon once wrote me that new data change the story one tells. It is, he said, like putting together a picture puzzle. At first, you think the structure in front of you is a sailboat; but you add another piece, and—no, wait—it's a mountain. Psychologists call these alterations "Gestalt changes," and I think that we are seeing these changes in both our day-to-day interpretations of data and

in the entire field of developmental biology. We are seeing an inversion of relationships within the biological sciences. Genetics is more and more becoming a subset of development. Similarly, the dynamic of evolution is being studied as a question of gene expression as well as gene frequencies. And developmental biology may be on the threshold of changing medicine as much as microbiology did at the turn of the twentieth century.

I began the Preface of the last edition with a quotation from the Grateful Dead, recalling "What a long, strange trip it's been." The epigram for this edition might be Eminem's "Be careful what you wish for." We may achieve biological powers that are "tenfold" what we had hoped to have. And it is axiomatic for this generation that "with great power comes great responsibility."

I hope this Ninth Edition of *Developmental Biology* presents a better way of teaching and learning (and questioning) developmental biology. The introductory section has been streamlined from six chapters to three—one each on developmental anatomy, the mechanisms of gene regulation during differentiation, and cell-cell communication during morphogenesis. Another new feature is the addition of short part-opening "chaplets" that address key concerns in developmental biology. These provide an introduction to the subsequent chapters, placing the forthcoming information into a specific context. Each chapter ends with a guide to web-based resources relevant to that chapter's content, and the Ninth Edition is the first to include an extensive glossary of key terms.

During the writing of this edition, I re-read some of the papers written by the first generation of experimental embryologists, scientists who were experiencing a Gestalt change as important as what we are experiencing today. What impressed me was not necessarily their answers (although some of them were remarkably good even by today's standards); rather, it was their asking the "right" questions. Some of their research did not give us any answers at all. But the results told the next generation of biologists what questions to ask. These embryologists stood in awe of the complexity of the embryo; yet they began to remove, transplant, destroy, and recombine cells in order to find out just how the fertilized egg could give rise to a structured body composed of different cell types. They had faith that these were scientific questions and that science would eventually be able to answer them.

The glory of developmental biology is that we now have interesting answers to many of their questions. But numerous questions that were asked a century ago still lack answers. How does the human brain become organized so that we can think, plan, recall, interpret, hate, and love?

How is the development of plants and insects timed so that the flower opens at the same time when its pollinator has left its cocoon? How does exercise increase muscle mass, and how does our face come to resemble those of our parents more than any one else's? To these questions, we have only very partial answers, but we are on our way.

Developmental biology presents a nascent scientist with a host of fascinating questions that are worth solving. And that's the invitation this book offers. One can enter developmental biology through many portals—genetics, cell biology, embryology, physiology, anatomy—and with many valid motivations. This is a field that needs the help of people with all sorts of competencies and talents. It is an old field that is itself undergoing metamorphic change and emerging as a new field that welcomes newcomers with open arms—full of questions.

Acknowledgments

In addition to the remarkable reviewers listed below, whose candid and thorough criticisms of early chapter drafts made this book so much better, there are some people whose help was absolutely critical. In particular, David McClay and Bill Anderson gave me many suggestions that were outstandingly important in constructing this edition. I also appreciate enormously the cooperation from all those scientists who sent me their photographs, and who even told me about others they had seen. The graphics of this book are truly amazing, and this is due to the community of developmental biologists.

The book's beauty and success is also the result of Andy Sinauer's vision and the hard work of the immensely talented staff he has assembled at Sinauer Associates. David McIntyre's ability to find appropriate photographs from the public and private databases is almost uncanny. Chris

Small and Janice Holabird of Sinauer's production department have put together the artwork, the photographs, and the text into a format that is both informative and pleasing. For a book of this size, this is a heroic undertaking. And, more than any other edition of this book (and she has been with it since its inception), this incarnation has been a collaborative effort with my editor Carol Wigg. The book seems to have become a full-time job for both of us.

I especially wish to thank Dr. Hannah Galantino-Homer of the University of Pennsylvania School of Veterinary Medicine, who took it upon her shoulders to compile a glossary for this book. Numerous people have said that they wanted such a glossary for their students, and putting one together is an extremely difficult task, involving an enormous amount of thought and expertise.

This textbook officially entered the "electronic age" in the mid 90s, and its web segment, www.devbio.com, has grown more important with each subsequent edition. With this edition, the *vade mecum*³ companion that debuted in 2002 is also on the web. Mary Tyler and Ron Kozlowski not only created *vade mecum*³, with its laboratory sections and its introductions to model animals, they have also produced interviews and filmed the techniques of several developmental biologists. You really have to see these films to realize what a valuable resource these are.

I am blessed by teaching some remarkable students who have not been shy about offering constructive criticism. Their suggestions will, I hope, benefit the next round of students.

And finally, this revising process has taken much longer than expected. I apologize to my wife, Anne Raunio, who has had to put up with me through it all, and to my friends, who may have wondered where I've been. I'll be back.

SCOTT F. GILBERT

Reviewers OF THE NINTH EDITION

It is no longer possible (if it ever was) for one person to comprehend this entire field. As Bob Seger so aptly sings, “I’ve got so much more to think about ... what to leave in, what to leave out.” The people who help me leave in and take out the right things are the reviewers. Their expertise in particular areas has become increasingly valuable to me. Their comments were made on early versions of each chapter, and they should not be held accountable for any errors that may appear.

Arkhat Abzhanov, *Harvard University*

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Media and Supplements

to accompany *Developmental Biology*, Ninth Edition

eBook (ISBN 978-0-87893-412-6)

www.sinauer.com/ebooks

New for the Ninth Edition, *Developmental Biology* is available as an online interactive ebook, at a substantial discount off the list price of the printed textbook. The interactive ebook features a variety of tools and resources that make it flexible for instructors and effective for students. For instructors, the eBook offers an unprecedented opportunity to easily customize the textbook with the addition of notes, Web links, images, documents, and more. Students can readily bookmark pages, highlight text, add their own notes, and customize display of the text. In addition, all of the in-text references to the Companion Website Web topics and to *DevBio Laboratory: vade mecum*³ are integrated into the ebook as direct links, so the student can easily access a wealth of additional material as they read.

Also available as a CourseSmart eBook (ISBN 978-0-87893-409-6). The CourseSmart eBook reproduces the look of the printed book exactly, and includes convenient tools for searching the text, highlighting, and notes. For more information, please visit www.coursesmart.com.

For the Student

Companion Website

www.devbio.com

Available free of charge, this website is intended to supplement and enrich courses in developmental biology. It provides more information for advanced students as well as historical, philosophical, and ethical perspectives on issues in developmental biology. Included are articles, movies, interviews, opinions, Web links, updates, and more. References to specific website topics are included throughout each chapter as well as at the end of each chapter.

*DevBio Laboratory: vade mecum*³: An Interactive Guide to Developmental Biology

<http://labs.devbio.com>

MARY S. TYLER and RONALD N. KOZLOWSKI

New for Version 3, *DevBio Laboratory: vade mecum*³ is now online. Access to the program is included with every new

copy of the textbook. (See the inside front cover for details.) *DevBio Laboratory: vade mecum*³ is a rich multimedia learning tool that helps students understand the development of the organisms discussed in lecture and prepares them for laboratory exercises. It also includes excerpts from the *Differential Expressions* series of videos, highlighting some major concepts in developmental biology, famous experiments, and the scientists who performed them.

Developmental Biology: *A Guide for Experimental Study, Third Edition*

MARY S. TYLER

(Included in *DevBio Laboratory: vade mecum*³)

This lab manual teaches the student to work as an independent investigator on problems in development and provides extensive background information and instructions for each experiment. It emphasizes the study of living material, intermixing developmental anatomy in an enjoyable balance, and allows the student to make choices in their work.

For the Instructor

(Available to qualified adopters)

Instructor's Resource Library

The *Developmental Biology*, Ninth Edition Instructor's Resource Library includes a rich collection of visual resources for use in preparing lectures and other course materials. The IRL includes:

- All textbook figures (including photos) and tables in JPEG (high and low resolution) and PowerPoint® formats
- A collection of videos illustrating key developmental processes
- Chick embryo cross-sections and chick embryo whole-mounts from *DevBio Laboratory: vade mecum*³ (PowerPoint® format)
- Video segments from *DevBio Laboratory: vade mecum*³
- Instructor's Reference Guide for *Differential Expressions*²

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