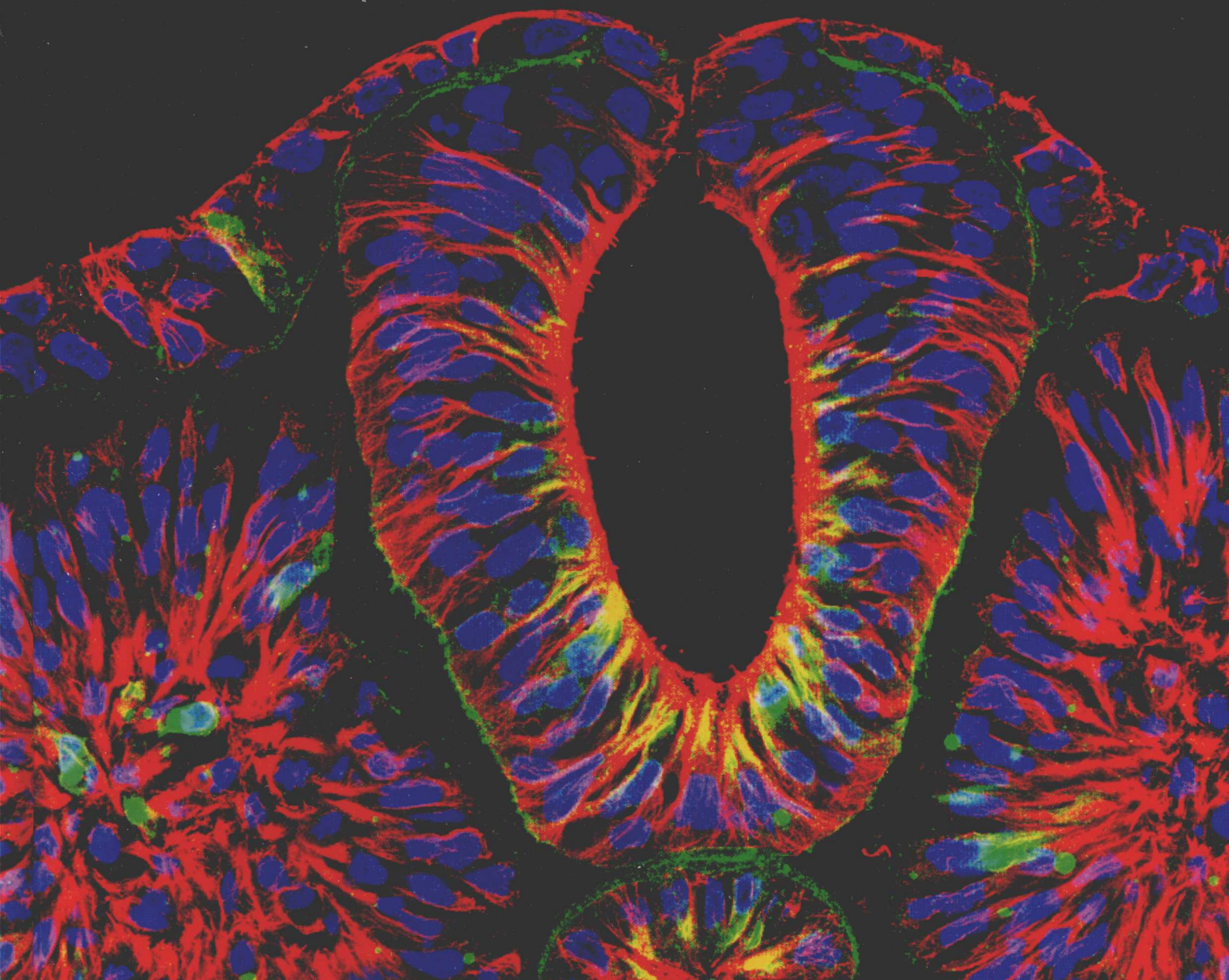
# Developmental Biology

TENTH EDITION

SCOTT F. GILBERT



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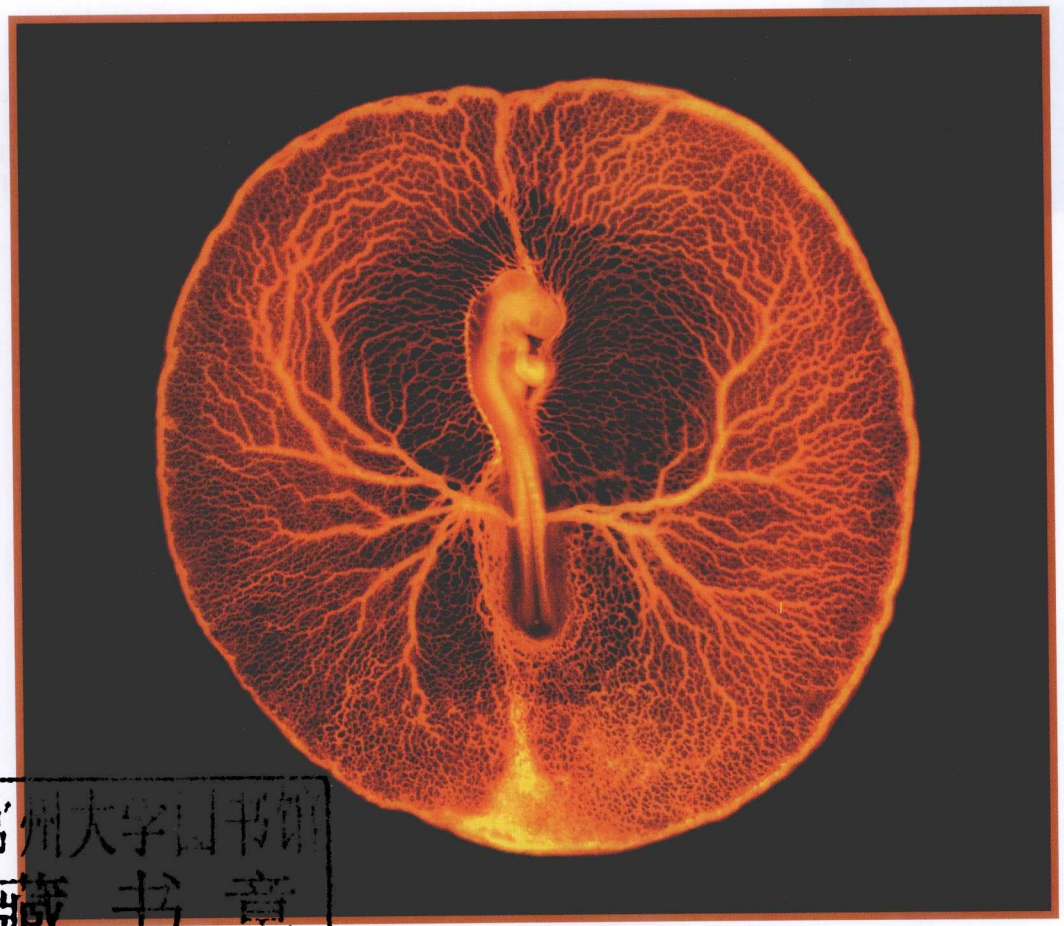



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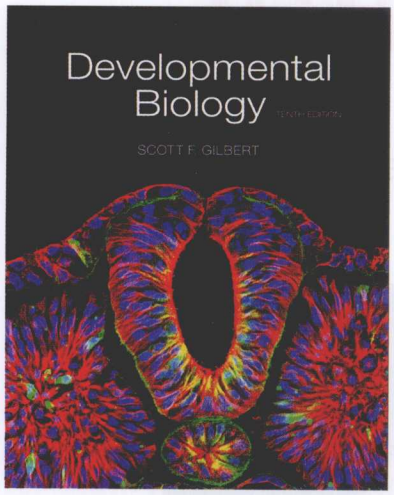


## The Cover

Cross-section of neural tube formation in a 2-day chick embryo. This confocal micrograph shows the neural tube (which will become the animal's central nervous system) closing at its most dorsal (top) region. The blocks of cells on either side are the somites, which will form muscles, vertebrae, and dermis. The upper cells become the epidermis (outer skin). Cell nuclei are stained blue, the microtubules of the cytoskeleton are red, and the vitronectin of the extracellular matrix appears green. Photograph by M. Angeles Rabadán and Elisa Martí Gorostiza, Instituto de Biología Molecular de Barcelona-CSIC.

## The Title Page

Fluorescence micrograph of a late 2-day chick embryo (about 45 hours after the egg was laid, at which point the heart has begun to beat). The vascular system of this embryo was revealed by injecting fluorescent beads into the circulation. The three-dimensional effect was achieved by superimposing two separate images. Photograph by Vincent Pasque. Used with permission of The Wellcome Institute.

**Developmental Biology**, 10th Edition



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*To Daniel, Sarah, David, and Natalia*

# Preface

*Change is the law of life. And those who look only to the past or present are certain to miss the future.*

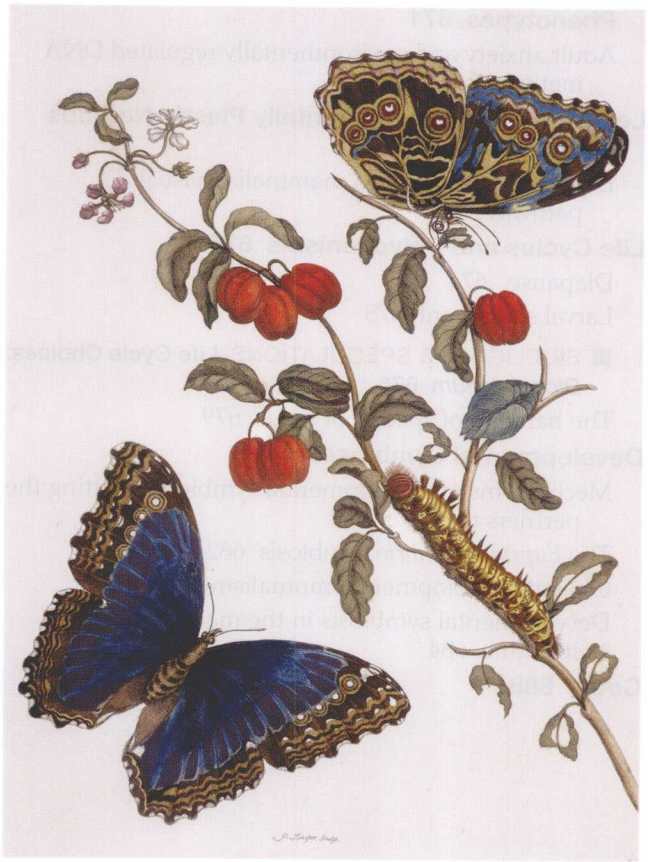
JOHN FITZGERALD KENNEDY (1963)

Metamorphosis is a time of redefinition and dramatic developmental transition. Caterpillars go from crawling and eating to flying and mating; tadpoles go from swimming to hopping, developing new muscles as their old ones decay. Today there's a feeling in the air that developmental biology is about to undergo another metamorphic molt. Don't panic!

I don't know what caterpillars experience as their new molt gives them wings. I don't know how a tadpole feels when it is about to become a frog. But I do know how developmental biology feels when it is about to undergo a major change, and this is how it feels today. It felt this way as I first wrote this textbook between 1980 and 1985. There were hints back then that developmental biology was about to change in a big way. Recombinant DNA was coming of age. It was becoming possible to identify and add new genes into an organism, and to take genes away. In 1985, the first edition of *Developmental Biology* had no mention of transcription factors or paracrine factors—but it mentioned the research that led to our discovery of them. Transcription factors entered the book's second edition three years later, and paracrine factors appeared in the next edition, three years after that. Between 1985 and 1991 the form of developmental biology changed from experimental embryology to developmental genetics. Our metamorphosis had occurred. Even journals changed their names.

My sense today is that the present metamorphosis will transform developmental genetics into an as yet unnamed developmental science that will integrate anatomy, physiology, genetics, cell biology, systems theory, genomics, and structural biology. Development has always been a science of syntheses and relationships, and these will be major themes for *all* science in the twenty-first century. Developmental biology will become a "biology without borders." The new developmental biology may be simultaneously molecular, ecological, evolutionary, and physiological. In fact, I would be surprised if it were not. As Mark Lewandoski told me at a recent meeting, "Developmental biology is dead. Long live developmental biology!"

Metamorphic change is in the nature of science. From within the larva, the rudiment of a new organism emerges. I hope this book helps to bridge those epistemes, the older and the newer way of approaching development. For me personally, the metamorphosis can hardly have occurred at a more appropriate time. Thirty years ago, as I started writing the first edition, I had a 2-year old child and a new job. Now that child has a 2-year old child and a new job. Revolution is nothing less than the turning of the cycle, and metamorphosis is the act of renewal. Long live developmental biology!



A plate from *Metamorphosis Insectorum Surinamensium* (1705) by the artist and scientist Maria Merian. She was one of the first scientists to document that caterpillars, pupae, and butterflies were different life cycle stages of a single organism.

## Acknowledgments

In book publishing, as in animal development, there are two types of relationships, the instructive and the permissive. Instructive relationships change the information in the product. They shape the phenotype. The reviewers listed on the following page have played this instructive role to great effect, letting me know what research is coming to the fore, reassuring me when my interpretations of data were sound, and correcting me when they were not. Such input both stabilizes and alters the content of the book, and to these reviewers I owe a huge debt of gratitude. If my book has some "OMG, how did he know that?" moments, the reviewers are the ones to credit. If there are any "WTF, why is this still being cited?" moments, I'm most likely the one to blame.

Permissive relationships don't change the information content, but enable that information to come into being. These are the transcription, translation, scaffolding and patterning apparatuses. Since the early editions of this book, my words, sentences, and paragraphs have been queried, clarified, rearranged, reordered, and realigned by Carol Wigg of Sinauer Associates. Carol's work on important biology textbooks deserves some kind of award for making biology accessible to the reader. It's an honor to have her work on my book. I have also been incredibly fortunate to have Elizabeth Pierson as copyeditor. She has an eagle eye, a sense of humor, and an uncanny ability to point out discrepancies hundreds of pages apart and make you smile at your own mistakes.

This is a beautiful book, and I can say that because it is not my doing. It is due in large part to the many wonderful photographs my generous colleagues continue to supply. It is also due to Chris Small and his production staff at Sinauer, especially designer Joan Gemme. Also at Sinauer, Johannah Walkowicz coordinated the academic reviews and course input for this revision, while Marie Scavotto and Nancy Asai of marketing made sure everyone knew the new edition was coming along.

The original vision of what this book could be and its evolution from its instar in 1985 has been directed by Andy Sinauer in collaboration with myriad reviewers and editors (and of course the author). Andy's many longstanding relationships with leading scientists (Andy doesn't "lose" authors) testify to his integrity and his standards for excellence, which have set a high bar few others can reach.

Like developmental biology, textbook publishing is undergoing a metamorphosis. I like to think this book helped usher in the age of electronic publishing when, back in the mid-1990s, we offered embedded websites in the text. The original website was a Gopher Wiki, and I had a map on my wall of all the biology websites then in existence. Today this book has its own large website, www.devbio.com, maintained by Jason Dirks, Nate Nolet, and the ever-growing number of Associates at Sinauer who work in multimedia and electronic formats. Among many other things, this expansive site allows the reader immediate access via links to PubMed to most of the original references cited in the book.

Also online is the wonderful Vade Mecum[3], created as a laboratory resource by Mary Tyler and Ron Kozlowski. This is the low-cost "electronic laboratory manual" for developmental biology laboratories, and it should also be looked at for its remarkable movie footage of the development of model organisms.

The administration of Swarthmore College and the University of Helsinki went above and beyond the call of duty in providing me with the facilities to write this book. Both venues remain full of stimulating people and great opportunities to continue learning. I have also been blessed with remarkable students who have never been shy about asking questions. Many of the footnotes in this book began as answers to questions posed by savvy students. Other footnotes attempt to highlight connections between developmental biology and other fields of study, particularly the perspectives offered by the humanities, which demand that we think about the context of what we do.

This is the tenth edition of *Developmental Biology*, and "what a long strange trip it's been." Either there is much more material to integrate than there used to be, or I'm getting older and slower (I'm sure it must be the former). The book is done, and I am looking forward to seeing my friends and family again! My wife, Anne Raunio, has been incredibly patient, and there seem to be all sorts of things around the house that need fixing.

SCOTT GILBERT

# Reviewers of the Tenth 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.

Ehab Abouheif, *McGill University*

Arkhat Abzhanov, *Harvard University*

William Anderson, *Harvard University*

Jonathan Bard, *University of Edinburgh*

Julie Brill, *University of Toronto*

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## to accompany **Developmental Biology,** Tenth Edition

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*Developmental Biology,* Tenth Edition is available as an eBook in several formats, all at a substantial discount from the price of the printed textbook. For details on available ebook formats, please visit the Sinauer Associates website at **www.sinauer.com**, or contact your Sinauer sales representative.

### For the Student

#### *Companion Website*

**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 in the printed textbook throughout each chapter, as well as at the end of each chapter.

#### *DevBio Laboratory: Vade Mecum³: An Interactive Guide to Developmental Biology*

**labs.devbio.com**

**MARY S. TYLER and RONALD N. KOZLOWSKI**

Access to *DevBio Laboratory: Vade Mecum*³ 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*² 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 students to make choices in their work.

### For the Instructor

**(Available to qualified adopters)**

#### *Instructor's Resource Library*

The *Developmental Biology,* Tenth 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 and tables in JPEG format (both high- and low-resolution versions), formatted for optimal projection quality
- PowerPoint® presentations of all figures and tables
- Chick embryo cross-sections and chick embryo whole-mounts from *DevBio Laboratory: Vade Mecum*³ (PowerPoint® format)
- Three collections of videos:
  - Developmental biology video collection
  - Video segments from *DevBio Laboratory: Vade Mecum*³
  - Video segments from *Differential Expressions*²
- Instructor's Reference Guide for *Differential Expressions*²

## Also Available

The following titles are available for purchase separately or, in some cases, bundled with the textbook. Please contact Sinauer Associates for more information.

- ***Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution***
  Scott F. Gilbert and David Epel
  Paper, 460 pages • ISBN 978-0-87893-299-3
- ***Bioethics and the New Embryology: Springboards for Debate***
  Scott F. Gilbert, Anna Tyler, and Emily Zackin
  Paper, 261 pages • ISBN 978-0-7167-7345-0
- ***Differential Expressions²: Key Experiments in Developmental Biology***
  Mary S. Tyler, Ronald N. Kozlowski, and Scott F. Gilbert
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# Brief Contents

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