PART ONE  GETTING STARTED  1

CHAPTER 1  OVERVIEW OF DEVELOPMENT  3

Chapter Preview

THE BASIC CONUNDRUM OF DEVELOPMENT 4

The Problem of Development Centers on Nonequivalent Cell Division
Cell Lineage and the Cellular Environment Influence Cell Fate
Box 1.1 Cell Communication
Assuming That All Cells in an Embryo Are Genetically Identical Is Justified
The Regeneration of Organs Often Involves the Respecialization of Cells
The DNA Sequences in Different Tissues Are the Same
Box 1.2 Recombinant DNA Technology (Cloning)

THE STUDY OF DEVELOPMENTAL BIOLOGY 13

This Textbook Is Organized into Three Parts
The Study of Development Is Circular
Box 1.3 Nucleic Acid Probes

KEY CONCEPTS
STUDY QUESTIONS
SELECTED REFERENCES

CHAPTER 2  GAMETOGENESIS, FERTILIZATION, AND LINEAGE TRACING  17

Chapter Preview

OOGENESIS 18

Female Gametes Are Formed in the Ovary
Oogenesis Is Characterized by Extensive Growth
Egg Formation Involves Meiosis
The Egg Is Highly Organized

Spermatogenesis 21
Male Gametes Are Formed in the Testis
Spermatogenesis Involves Formation of a Streamlined Cell

Fertilization 23
Fertilization Produces Two Distinct and Important Results
Both Gametes Are Activated at Fertilization
Activation of the Egg Involves the Cortex
Changes in Function of Egg Membrane Proteins Drive Egg Activation
Calcium Ion Release Is Essential for Egg Activation
Box 2.1 G Protein Signalling
Fertilization May Activate Protein Synthesis on Stored mRNA
Several Mechanisms Prevent Polyspermy

Tracing Cell Lineages 30
Lineage Tracing Is Essential to Understanding Development
Cleavage Is a Period of Rapid Mitosis

KEY CONCEPTS
STUDY QUESTIONS
SELECTED REFERENCES

PART TWO EARLY DEVELOPMENT OF ANIMALS 37

Chapter 3 Oogenesis and Early Development of Drosophila 39

Chapter Preview

Embryogenesis 40
The Formation of an Egg is a Prelude to Embryo Formation
Fertilization and Cleavage Initiate Embryo Formation
Box 3.1 Developmental Genetics
The Cellular Blastoderm Is Organized
Gastrulation is a Translocation of Surface Cells to the Interior
The Embryo Becomes Segmented
Box 3.2 Germ Layers

Patterning of the Embryo 50
Localized Determinants in the Egg Specify a Cell's Fate
Maternal Effect Mutants of Drosophila Encode Morphogens
The Anterior Morphogen Is Bicoid
The Posterior Pattern Is Determined by the Concentration of Nanos
The Morphogen for the Terminals of the Egg Is Torso
The Morphogen for Dorsoventral Organization Is Dorsal Protein
The Patterning of the Follicle Cells Drives the Patterning of the Oocyte

KEY CONCEPTS

STUDY QUESTIONS

SELECTED REFERENCES

CHAPTER 4  AMPHIBIAN DEVELOPMENT 59

Chapter Preview

GAMETOGENESIS 60
Oogenesis Involves Cyclic, Progressive Maturation of Oogonia
Genes for Ribosomal RNA Are Transiently Amplified
Box 4.1 Ribosome Formation and Structure
The Completion of Meiosis I Is Regulated By Progesterone
Spermatogenesis in Frogs Produces Four Spermatids

FERTILIZATION AND EARLY DEVELOPMENT 64
Fertilization Establishes Bilateral Organization in the Egg
Box 4.2 Using Embryos in Cell Biology
Cortical Rotation Involves Parallel Vegetal Microtubule Arrays
Cleavage Is a Period of Intense Cellular Assembly
The Midblastula Transition Is a Period Of Major Changes
Maps of the Late Blastula Reveal Distinct Identities
Vegetal Cells of the Blastula Induce Mesoderm from Animal Cells

GASTRULATION, GERM LAYERS, AND ORGANOGENESIS 71
Gastrulation Involves Massive Movements of Cell Groups
Bottle Cells Invaginate and Lead the Way for Involution
Gastrulation Establishes the Germ Layers
Dorsal Ectoderm Is Induced by Dorsal Mesoderm and Will Form a Neural Tube
Mesoderm and Endoderm Will Form Many Organs
Is All This Detail Really Necessary?

KEY CONCEPTS

STUDY QUESTIONS

SELECTED REFERENCES

CHAPTER 5  AMNIOTE DEVELOPMENT 79

Chapter Preview

OOGENESIS AND THE EARLY DEVELOPMENT OF BIRDS 80
Gametogenesis in Birds Involves Specialization of the Female Reproductive Tract
The Newly Laid Hen's Egg Has Invisible Axis
The Area Pellucida Becomes a Two-Layered Structure
Does the Hypoblast Influence the Organization of the Epiblast?
GASTRULATION IN BIRDS 84
The Epiblast is the Source of All Embryonic Germ Layers in Amniotes
The Anterior Border of the Primitive Streak Is Specialized
Hensen’s Node Organizes the Axis and Induces the Central Nervous System
Gastrulation Results in the Formation of an Archetypal Vertebrate Axis
The Extraembryonic Membranes of Birds Are Comprised of Four Membranous Sacs

EARLY MAMMALIAN DEVELOPMENT 88
Oogenesis, Fertilization, and Cleavage in Mammals Involve Specialization of the Oviduct
Cleavage Produces a Blastocyst That Will Embed in the Lining of the Uterus
Signaling Pathways May Be Elucidated by the Use of Dominant Negatives
The Formation of the ICM Is a Strategy Unique to Mammalian Embryos
The Mouse Embryo Possesses an Unusual Morphology
The Epiblast Is the Source of Embryonic Germ Layers

MAMMALIAN ADAPTATIONS 94
At the End of Gastrulation, the Morphology of Mammalian Embryos Is Similar to That of Birds, but
the Extraembryonic Membranes Differ
The Trophoblast Will Help Form the Placenta

MANIPULATING MOUSE EMBRYOS 96
Allophenic Mice Provide an Opportunity to Understand the Cellular Dynamics of the Early Embryo
Cells Injected into the Blastocyst Cavity Can Also Form Chimeras, Which is the Basis for Creating
Transgenic Mice

PART THREE VERTEBRATE ORGANOGENESIS 101

Chapter 6 DEVELOPMENT OF ECTODERMAL DERIVATIVES IN VERTEBRATES 103

Chapter Preview

THE NEURAL PLATE 104
The Ectoderm Is the Source of the Nervous System and the Skin
The Neural Plate Results from the Induction of Ectoderm
The Arising Neural Plate Is Organized
Dorsoventral Patterning of the Neural Plate and Tube Is Driven by Localized Release of the Growth Factor Sonic Hedgehog

THE NEURAL CREST 110
The Neural Crest Is a Multipotential Population of Migratory Cells
The Differentiation of Neural Crest Cells Is Determined Largely by Their Location
Box 6.1 Cells in the Nervous System
Chapter 9  **Plant Meristems**  177

**Chapter Preview**

**Shoot Meristems**  178

- Meristems Have a Characteristic Histological Organization
- Meristems Produce Patterns of Organs (Phyllotaxy)
- Cell Expansion Is Very Important in Leaf Initiation
- Box 9.1 Arabidopsis
- Apical Dominance Influences Development of Axillary Meristems
- Box 9.2 Genes That Function in the Evolution of Maize
- The Meristem Establishes Leaf Dorsoventrality

**Root Meristems**  188

- Root Apical Meristems Produce Radial Patterns
- Lateral Root Meristems Arise from Differentiated Cells

**Chapter 10  Reproduction in Plants**  192

**Chapter Preview**

**Floral and Inflorescence Meristems**  192

- Flowering Is Regulated by Daylength
- Floral Meristems Initiate Floral Organs
- Floral Organs Initiate in Whorls
- Box 10.1 Putting Genes into Plants

**The Alternation of Generations: The Haploid-Diploid Life Cycle in Plants**  199

- In Flowering Plants, the Gametophyte Stage Is Abbreviated
- A Double Fertilization Is Involved in the Making of a Seed
Proteoglycans Are Unusual Protein–Polysaccharide Molecules Inhabiting the Matrix
A Plant Cell Wall Is an Assemblage of Cellulose and Amylopectin
Specific Integral Membrane Molecules Bind to Both Matrix Molecules and Intracellular Proteins

EPITHELIAL CELLS AND JUNCTIONS 239

Epithelial Cells Are Joined by Specific Junctions
Receptor Molecules Also Exist as Integral Membrane Proteins in Both Mesenchyme and Epithelium
G Protein–linked Receptors Are Important in Development
Receptors, Ligands, and Intracellular Signal Transduction Pathways Are Important in Regulating Development

CELL ADHESION 243

Cell–Cell and Cell–Matrix Adhesion Play a Role in Morphogenesis
Several Classes of Specific Cell Adhesion Molecules Exist
The Function of Cell Adhesion Molecules May Be Analyzed in Their Cellular Context

MORPHOGENETIC MANEUVERS 246

There Are Eight Basic Morphogenetic Movements
Cell Motility and Protrusive Activity Involve Attachment to a Substrate
Changes in Cellular Shape Are Crucial in Determining Form
Rates of Cell Proliferation Influence Tissue Shape
Cell Division Planes Affect Morphogenesis
Cell Adhesion Is Crucial in Morphogenesis
What Is Cause and What Is Effect in Morphogenesis
Experiments Using Inhibitors of Cell Function Are Useful but Difficult to Interpret

KEY CONCEPTS
STUDY QUESTIONS
SELECTED REFERENCES

CHAPTER 13 TISSUE INTERACTIONS AND MORPHOGENESIS 253

Chapter Preview

CHANGES IN MOTILE BEHAVIOR 254

The Homing of Primordial Germ Cells Involves Receptor Tyrosine Kinases
The Migration of Neural Crest Cells Is Governed by Several Factors
Neural Crest Migration Is Sensitive to Ephrins
Growth Cone Activity Drives Neurite Outgrowth
Cell–Cell and Cell–Matrix Interactions May Help Direct Neurite Outgrowth
Netrins Can Serve as Chemoattractants
Semaphorins Are a Large Family of Chemorepellents
The Connections Between Retina and Tectum Are Guided in Part by Ephrins

EPITHELIAL–MESENCHYAL INTERACTIONS 262

Limb Outgrowth Requires Reciprocal Tissue Interactions
Branching Morphogenesis in the Lung and Salivary Gland Requires Tissue Interactions
Kidney Morphogenesis Requires Complex Circuits of Interactions Between Interacting Tissues
GASTRULATION REVISITED 267

Gastrulation in the Sea Urchin Involves Many Changes in Cellular Behavior

Box 13.1 Sea Urchin Development

Gastrulation in Xenopus Is Also a Multicomponent Process
Convergent Extension Drives Involution
Fibronectin Aids Migration of Involuting Cells
Some Mutations in Drosophila Disrupt Gastrulation

KEY CONCEPTS

STUDY QUESTIONS

SELECTED REFERENCES

PART SIX  REGULATION OF GENE EXPRESSION  279

CHAPTER 14  THE LEVELS OF REGULATION OF GENE EXPRESSION IN DEVELOPMENT  281

CHAPTER PREVIEW

TRANSCRIPTIONAL REGULATION  282

Transcription Uses Chromatin as a Substrate
Methylation of DNA Can Keep Chromatin Inactive
Methylation Imprints Genes in Mammals
RNA Polymerase Must Associate with General Transcription Factors to Become Functional
Activator and Suppressor Proteins Regulate the Initiation of Transcription
The endo6 Gene of Sea Urchin Embryos Illustrates How Regulatory Sequences Act Like a Microprocessor
Box 14.1 Using Reporters to Study the Regulation of Transcription
Transcription of the β-Globin Gene Family Is Regulated by a Complex Remote Control Element

TRANSLATIONAL REGULATION  290

Posttranscriptional Steps Must Occur Before Translation Can Happen
The Regulation of mRNA Translation During Development Is Common and Involves Various Mechanisms
Translation of MRNAs Made During Oogenesis Is Regulated
Messenger RNAs Can Be “Masked” and Polyadenylated
 Messenger RNAs May Be Localized to Specific Parts of the Cell
Nanos mRNA Is an Example of Localized mRNA
Box 14.2 Genomics and Chips

POSTTRANSLATIONAL REGULATION  295

Protein Modifications Can Be Nodes of Developmental Control
The Hedgehog Ligand Is Posttranslationally Modified
Esterification of Hedgehog Can Possibly Restrict Its Diffusion
Diffusion of Sonic Hedgehog Is Important for Vertebrate Development
Vgl., a Localized Ligand Implicated in Early Xenopus Development, Has to Be Processed to Be Active
The Assembly of Proteins into Macromolecular Complexes Constitutes Another Level of Regulation of Gene Expression
CHAPTER 15 DEVELOPMENTAL REGULATORY NETWORKS I: DROSOPHILA AND OTHER INVERTEBRATES 302

Chapter Preview

GENERATING NONEQUIVALENT CELLS 303
- Developmental Networks Are Complex
- Asymmetric Cell Divisions in Yeast Give Us Clues
- Asymmetric Cell Division in the Early C. elegans Embryo May Result from Cell Signaling
- Asymmetric Divisions of Neuroblast and Sensory Organ Precursors Utilize Cytoskeletal Cues
- Inhibitory Signaling Between Cells Is a Common Mechanism in Development
- The Machinery Used to Establish Asymmetry Is Complex, yet Its Use Is Widespread

ESTABLISHING THE SEGMENTS IN DROSOPHILA 309
- Morphogens Initiate Differential Gene Expression
- Gap Genes Establish Seven Broad Stripes
- Box 15.1 Establishment of Axial Polarity in Drosophila: A Summary
- Pair-Rule Genes, Activated by Gap Genes, Create Seven Repetitive Stripes
- Pair-Rule Genes Have Complex Regulatory Regions
- The Gene eve Is Regulated by Both Activating and Inhibitory Interactions
- Segment Polarity Genes Subdivide the Seven Stripes
- Box 15.2 Methods for Studying Gene Interactions
- Expression of the Segment Polarity Genes Provides Permanent Markers for Parasegmental Boundaries
- Intercellular Communication Involving Engrailed Keeps Its Expression “On”

HOMEOTIC SELECTOR GENES AND PARASEGMENT IDENTITY 321
- The Bithorax Complex Dictates Thoracic and Abdominal Segment Identity
- The Antennapedia Complex Controls Anterior Segment Identity
- Other Homeotic Genes Specify Head and Posterior Parts
- How Do the Homeotic Genes Function?

PATTERNING THE WING 327
- Wing Development Is Governed by Cellular Interactions
- Anteroposterior (A/P) Patterning Depends on Intercellular Signaling
- Patterning of the Dorsoventral (D/V) Compartments of the Wing Is Also Governed by Cellular Interactions
- How Does the Developing Embryo Establish Local Patterns of Organ Formation?

KEY CONCEPTS
STUDY QUESTIONS
SELECTED REFERENCES
CHAPTER 16 DEVELOPMENTAL REGULATORY NETWORKS II: VERTEBRATES 334

CHAPTER PREVIEW

SIGNALING AND DEVELOPMENT 335

A Frog Is Not a Fly
Many Signaling Molecules and Transcription Factor Domains Are Found in Virtually All Animals

THE NIEUWKOOP CENTER REVISITED 336

The Nieuwkoop Center Is a “Dorsalizing” Center
Box 16.1 Zebrafish
The siamois Gene Is a Reliable Indicator of Nieuwkoop Center Activity
The Transcription Factor Gene vegT Also Plays a Role in Germ-Layer Specification

THE SPEMMANN ORGANIZER REVISITED 341

The Spemann Organizer Arises as a Consequence of Nieuwkoop Center Activity
The Spemann Organizer Has Distinctive Gene Expression and Secretes Many Ligands
The Spemann Organizer Is a Neuralizing Center
The Spemann Organizer Provides Anteroposterior Neural Patterning
The Spemann Organizer Also Dorsalizes Mesoderm
Antagonisms Between Ventralizing and Dorsalizing Factors Pattern the Mesoderm

MORPHOGENS 347

Morphogens Are Involved in Positional Information
BMPs and Activin Are Morphogens
Left-Right Body Patterning Also Involves Signaling Pathways

AMNIOTE HOX GENES 351

Amniote Embryos Use Similar, but Not Identical, Regulatory Networks
Homeotic Selector Genes Are Present in Vertebrates as Well as Drosophila
HOX Genes Function as Selector Genes

SIGNALS IN LIMB DEVELOPMENT 355

HOX Genes and Signaling Pathways Play Important Roles in Limb Development
Limb Bud Placement Is Probably Regulated by Several Factors
Dorsalventral Organization Is Mediated by a D/V Compartmenal Boundary
Anteroposterior Patterning Is Controlled by Sonic Hedgehog
P/D Patterning Requires Ectoderm and Mesoderm
HOX Genes May Regulate Limb Differentiation

KEY CONCEPTS
STUDY QUESTIONS
SELECTED REFERENCES
CHAPTER 17  EVOLUTION AND DEVELOPMENT 363

CHAPTER PREVIEW

DEVELOPMENT AND EVOLUTION 363

Are There Laws of Development?
There Is a Close Link Between the Study of Development and the Study of Evolution
Molecular Biology and Genetics Have Invigorated the Relationship Between Development and Evolution

CONSERVATION OF GENES AND NETWORKS 364

Many Genes Important in Development Are Conserved
Useful Motifs Are Conserved
Entire Signaling Pathways Are Conserved
The HOM/HOX Complex Illustrates the Partial Conservation of Selector Genes
The Gene ubx Helps Govern the Formation of Butterfly Wings
Box 17.1 The Hox Cluster
Vertebrates Have Altered Patterns of Hox Gene Expression
Limblessness in Snakes Involves Changes in Hox Gene Expression

THE PHYLOTYPIC STAGE 372

A Phylotypic Stage Exists in the Postgastrula Embryos of Many Animal Phyla
In Chordates, the Phylotypic Stage Is the Pharyngula
Development Up to the Pharyngula Stage Takes Place in Different Ways
Development After the Pharyngula Stage Generates Great Diversity

DIVERSIFICATION OF SIGNALING SYSTEMS 375

Vertebrate Limbs Provide an Example of Postphylotypic Diversity
Signaling Systems May Adopt New Roles in Different Animal Groups
Signaling Systems May Themselves Be Modifiable

LARVAE AND EVOLUTION 378

Many Animals Develop Indirectly from Within a Larva
HOX Genes in Sea Urchins Are Expressed in Set-Aside Cells
The Linkage Between Direct and Indirect Development May Not Be So Complex
Changes in Relative Timing of Developmental Processes Can Create Substantial Differences in Organisms

NOVELTY 381

Some Radical Changes in Body Plan May Not Be So Complex
Apparent Similarities May Mask Regulatory Differences
The Neural Crest Is a Vertebrate Invention
Developmental Strategies Generate Organismal Novelty

KEY CONCEPTS

STUDY QUESTIONS

SELECTED REFERENCES

STUDY ANSWERS 387

PHOTO CREDITS 393

INDEX 395