Brief Contents

PART I: CONTEXT AND FOUNDATIONS

1 Evolution and Embryology: A Brief History of a Complex Pas de Deux 3

2 Information Sources for Reconstructing Developmental Evolution: I. Fossils 35

3 Information Sources for Reconstructing Developmental Evolution: II. Comparative Molecular Studies 65

4 Genetic Pathways and Networks in Development 99

5 Conserved Genes and Functions in Animal Development 127

PART II: CASE STUDIES IN PATHWAY EVOLUTION

6 Evolving Developmental Pathways: I. Sex Determination 173

7 Evolving Developmental Pathways: II. Segmental Patterning in Insects 205

8 Evolving Developmental Pathways: III. Two Organ Fields: The Nematode Vulva and the Tetrapod Limb 255

PART III: CONUNDRUMS

9 Genetic Source Materials for Developmental Evolution 309

10 Costs and Constraints: Factors that Retard and Channel Developmental Evolution 363

11 On Growth and Form: The Developmental and Evolutionary Genetics of Morphogenesis 393

12 Speciation and Developmental Evolution 441

13 Metazoan Origins and the Beginnings of Complex Animal Evolution 467

14 The Coming Evolution of Evolutionary Developmental Biology 503
Contents

PART I: CONTEXT AND FOUNDATIONS  1

1  Evolution and Embryology: A Brief History of a Complex Pas de Deux  3

Introduction: Birth of a Scientific Field  3
BOX 1.1  CLONING HOX GENES  6
Identifying the Paradox; Defining a Framework  8
Contemplating a History  11
Morphology and Embryology in the 19th Century  13
Darwin’s “Revolution”  19
The Fractured Mirror: Biology between 1900 and the 1930s  22

The Modern Synthesis and the Further Eclipse of Embryology  24
Specialization within Biology  25
Typological versus Population-Based Thinking  25
Large versus Small Differences  25
Nucleus versus Cytoplasm  26
BOX 1.2  FISHER’S ARGUMENT ON THE IMPORTANCE OF MUTATIONS OF SMALL VERSUS LARGE EFFECT  27
Personalities  28
Evolutionary Developmental Biology  31
Summary  34

2  Information Sources for Reconstructing Developmental Evolution: 1. Fossils  35

Introduction: Two Kinds of Evidence  35
The Essentiaity of Fossil Evidence  37
BOX 2.1  ON GEOCHRONOLOGY AND STRATIGRAPHY  39
Expanding the Known Universe of Developmental Evolutionary Events  41
Phylogenetic Reconstruction  42
Phylogenetic Systematics  42
Cladistics, Fossils, and the Mapping of Events  46

Identifying Changes in Developmental Processes: Examples from Dinosaur Evolution  51
BOX 2.2  TERMINOLOGICAL SHIFTS IN THE MEANING OF HETEROCHRONY  54
Fossil Evidence and the Elucidation of “Novelties”  57
BOX 2.3  KEY INNOVATIONS  61
Summary  64
3 Information Sources for Reconstructing Developmental Evolution: II. Comparative Molecular Studies 65

Introduction: Tracing Genetic Changes in Development 65
Gene Evolution and Developmental Evolution: A Complex Set of Relationships 66
The Analytical Problem: Identifying Orthologues 67
The Substantive Issue: Changing Gene Functions in Evolution 67
BOX 3.1 GENE DUPLICATIONS AND GENE FAMILIES 68
The Analytical Opportunity: Molecular Clocks 71
Direct Development in Sea Urchins and Frogs: Mapping Evolutionary Changes in Early Development 71
Direct Development and the Overthrow of a Long-Held Supposition 80
Direct Development as a Window on Mechanisms of Early Embryogenesis 81
Charting the Changes in Genetic Circuitry 85
The Craniate Head: Reconstructing the Cellular and Genetic Sources of an Evolutionary Novelty 87
Comparative Anatomical Studies 91
Gene Expression Studies 91
Genetic Bases of the Evolutionary Elaboration of Structure 96
Summary 98

4 Genetic Pathways and Networks in Development 99

Introduction: Developmental and Genetic Pathways 99
Biochemical Pathways: From Garrod to Beadle and Ephrussi 101
Developmental Pathways: Waddington’s Contribution 105
Microbial Genetics and the Birth of Saturation Mutant Hunting 108
Genetic Pathways for Pattern Formation and Sex Determination 110
Pathway Analysis: The Perils of Simplicity 114
Functional Redundancy 114
Pleiotropy 117
Cautionsary Notes in Thinking about Genetic Pathways 118
From Pathways to Networks 118
Does the Genetic Pathway Concept Apply Only to Highly Canalized Systems? 122
Summary 125

5 Conserved Genes and Functions in Animal Development 127

Introduction: Visible Diversity versus Shared Genetic Identities 127
Hox Genes and Antero-Posterior Patterning 129
Gene and Cluster Size 135
Cluster Number 135
Gene Order and Content 136
Developmental Roles 136
Dorso-Ventral Patterning 137
Conservation of Genes and Gene Function in the CNS 141
BOX 5.1 ECTOPIC EXPRESSION 144
Conservation of Genes and Gene Functions in Heart and Eye Development 145
Conserved Heart Development Genes 145
Pax6 and the Evolution of Eye Structures 148
PART III: CONUNDRUMS 307

9 Genetic Source Materials for Developmental Evolution 309

Introduction: Gene Recruitment 309
Categories of Genetic Variation 313
Primary Recruitment Events and Promoter Evolution 316
Mutation in, and Evolution of, Promoter Sequences 316
Examples of Enhancer Mutations that Alter Development 323
Creation of New cis-Acting Enhancer Sites for Transcriptional Control 324
Multiplying Resources for Gene Recruitment: Gene Duplications and the Growth of Gene Families 327
Processes that Shape Gene Family Evolution 329
The Evolution of Sequence Diversity and New Functions within the Hox Genes 333
Gene Duplication and Stabilization of Developmental Roles 338
Polyploidy as the Extreme Version of Gene Duplication 345
Gene and Genome Duplications as Resources for Genetic Pathway Evolution 347
A Note on Modularity and Entrainment, or What the Classic Neo-Darwinian View Missed 348
Hiding and Sorting Variation: Canalization and Genetic Assimilation 350
Summary 360
10 Costs and Constraints: Factors that Retard and Channel Developmental Evolution 363

Introduction: The Winners’ Circle 363
Selective Processes and Developmental Evolution 367
Genetic Variation as a Rate-Limiting Factor in Gene Recruitment and Developmental Evolution 369
New Genetic Variation as Rate-Setter of Evolutionary Change? 369
Gene Recruitment: Potential Costs and Barriers 371
Enhancer Properties and Their Implications for Gene Recruitment 372
Partitioning the Selection Coefficient 377
Gene Products Caught in Adaptive Conflict 379
Is There a Selective Hurdle in Initial Expression of Recruited Transcription Factor Genes? 381
Physical, Physiological, and Developmental Constraints 383
Summary 392

11 On Growth and Form: The Developmental and Evolutionary Genetics of Morphogenesis 393

Introduction: The Influence of Physical Forces 393
Physical Factors in Morphogenesis and the Roles of Gene Products 398
From Matrix Products to Morphogenesis 398
Morphogenesis of Cell Masses: Physical Factors and Genetic Influences 407
Evolutionary Changes in Morphogenetic Processes 413
Influences of Gene Products on Morphogenesis: Generalizing the Picture 415
From Morphometrics to Evolutionary Developmental Genetics 419
Stage 1: Quantitative Analyses of Growth 420
Stage 2: Allometry and Evolutionary Questions 422
Stage 3: Moving Into the Cell: The Cell Cycle 425
Stage 4: Charting the Complexity of Internal and External Controls of the Cell Cycle and of Cell Proliferation 427
Stage 5: Moving toward a Developmental Genetics of Growth Control 429
Synthesizing Morphometrics, Genetics, Development, and Evolution 434
Evolutionary Quantitative Genetics and Growth Control 434
BOX 11.1 QUANTITATIVE TRAIT LOCI 435
The Development of Teeth as a Paradigm of Morphological Evolution 436
Summary 439

12 Speciation and Developmental Evolution 441

Introduction: Two Linked Phenomena 441
Speciation, Reproductive Isolation, and Developmental Change 444
The Allopatric versus Sympatric Speciation Debate and Developmental Evolution 447
Sexual Selection and Developmental Evolution 450
Sexual Selection and Sympatric Speciation 450
Intersecting Genetic Controls of Sex Determination and Morphological Systems 455
# Contents

- **The Bateson–Dobzhansky–Muller Model of Speciation and a Recent Molecular Perspective** 459
- **Microevolution versus Macroevolution: How Different Are They?** 461
- **The Genetic Basis of Species versus Larger Taxonomic Differences** 462
- **Microevolution and Macroevolution as Dynamic Processes** 464
- **Summary** 465

## 13 Metazoan Origins and the Beginnings of Complex Animal Evolution 467

- **Introduction: A Few Rays of Light** 467
- **Fossil Evidence on the Beginnings of Animal Life** 470
- **Dating the Origins of the Metazoa by Molecular Clock Methods** 478
- **The New Molecular Phylogenetics of the Metazoa** 482
- **Stages of Complexity Increase in Early Metazoan Evolution** 487
- **Thinking about the Origins of the Bilateria** 494
- **The “Roundish Flatworm”: A View from the Fossil Beds of the Neoproterozoic** 494
- **Early Metazoans as Trochophore Larvae and the Origination of Set-Aside Cells: A View from Comparative Developmental Biology** 494
- **Planula Larvae as the Evolutionary Platform for the Bilateria: A View from a Systematics Perspective** 499
- **Summary** 500

## 14 The Coming Evolution of Evolutionary Developmental Biology 503

- **Introduction: An Analytical Framework** 503
- **Genetic Pathways and Networks: How Useful a Framework?** 505
- **Three Major Questions for the Future** 507
  - How Do Developmental Novelties Arise in Evolution? 508
  - How Do Microevolutionary Processes Differ from Macroevolutionary Processes? 509
  - What Factors Determine Rates of Developmental Evolution? 509
- **New Technologies and New Departures** 510
  - Detailed Promoter Comparisons of Orthologous Genes with Different Functions 511
- **Mapping Patterns of Total Gene Expression Change** 512
- **Quasi-Genetic Functional Tests** 514
- **Searches for Functional Relationships between Molecules: The Two-Hybrid Method** 517
- **BOX 14.1 THE “TWO-HYBRID” METHOD FOR DETECTING NEW FUNCTIONAL INTERACTIONS** 518
- **Prospects for Applying Functional Tests to Evolutionary Developmental Questions** 519
- **Additional Departures** 519
- **Synthesizing Paleontology and Molecular Genetic Studies** 522
- **Summary** 523

**Appendix 1: Genetic Nomenclature** 525

**Appendix 2: Reconstructing Phylogenetic History with Cladistics** 527

**Appendix 3: Molecular Clocks** 530

**Glossary** 533

**References** 541

**Index** 581

© Sinauer Associates, Inc. This material cannot be copied, reproduced, manufactured or disseminated in any form without express written permission from the publisher.