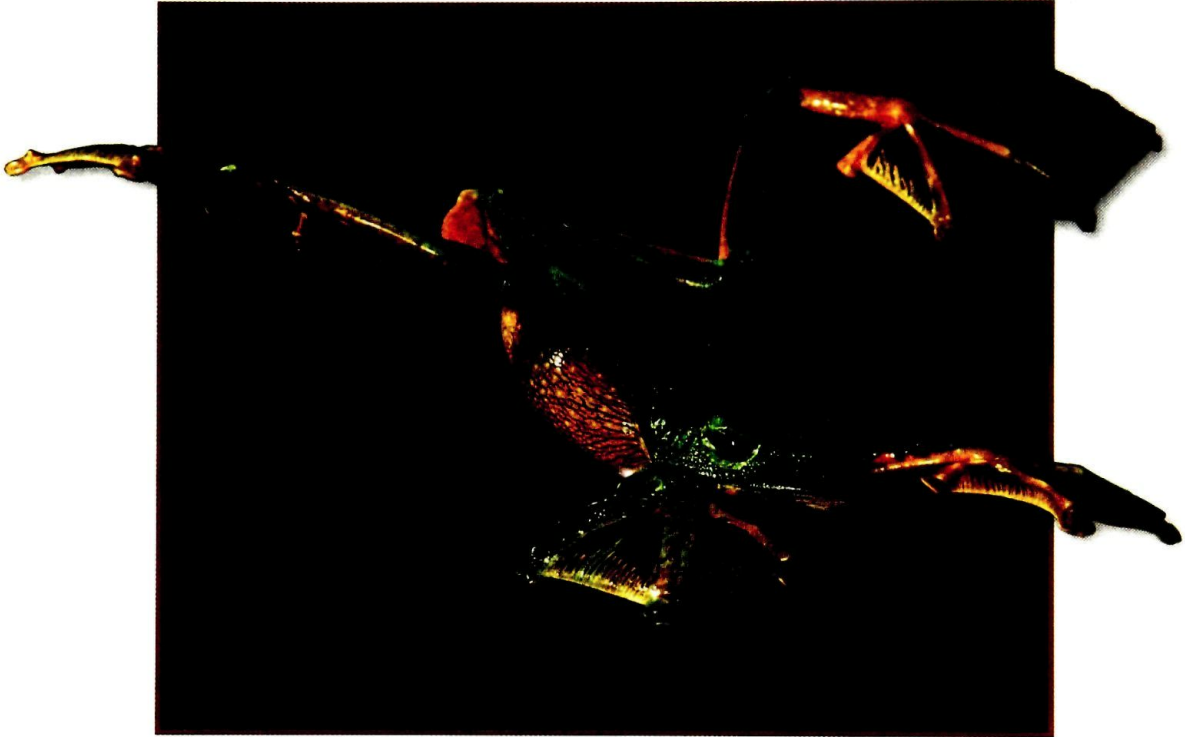


# evolution

SECOND EDITION



**DOUGLAS J. FUTUYYMA**

*Stony Brook University*

*Chapter 20, "Evolution of Genes and Genomes"*

*by Scott V. Edwards, Harvard University*

*Chapter 21, "Evolution and Development"*

*by John R. True, Stony Brook University*



**SINAUER ASSOCIATES, INC. • Publishers**  
*Sunderland, Massachusetts U.S.A.*

# Contents

## CHAPTER 1

---

### ***Evolutionary Biology 1***

- What Is Evolution? 2***
- Before Darwin 4***
- Charles Darwin 6***
- Darwin's Evolutionary Theory 7***
- Evolutionary Theories after Darwin 8***
- The Evolutionary Synthesis 9***
  - Fundamental principles of evolution 9
- Evolutionary Biology since the Synthesis 11***
- Philosophical Issues 12***
- Ethics, Religion, and Evolution 13***
- Evolution as Fact and Theory 13***

## CHAPTER 2

---

### ***The Tree of Life: Classification and Phylogeny 17***

- Classification 19***
- Inferring Phylogenetic History 22***
  - Similarity and common ancestry 22
  - Complications in inferring phylogeny 25
  - The method of maximum parsimony 27
  - An example of phylogenetic analysis 29
  - Evaluating phylogenetic hypotheses 31
- Molecular Clocks 33***
- Gene Trees 35***
- Difficulties in Phylogenetic Analysis 37***
- Hybridization and Horizontal Gene Transfer 42***

## CHAPTER 3

---

### ***Patterns of Evolution 45***

- Evolutionary History and Classification 47***
- Inferring the History of Character Evolution 48***
- Some Patterns of Evolutionary Change Inferred from Systematics 50***
  - Most features of organisms have been modified from pre-existing features 50
  - Homoplasy is common 53
  - Rates of character evolution differ 56
  - Evolution is often gradual 57
  - Change in form is often correlated with change in function 58
  - Similarity among species changes throughout ontogeny 58
  - Development underlies some common patterns of morphological evolution 59
- Phylogenetic Analysis Documents Evolutionary Trends 63***
- Many Clades Display Adaptive Radiation 64***
- Patterns in Genes and Genomes 66***
  - Genome size 66
  - Duplicated genes and genomes 67

## CHAPTER 4

---

### ***Evolution in the Fossil Record 73***

- Some Geological Fundamentals 73***
  - Plate tectonics 74
  - Geological time 74
  - The geological time scale 75
- The Fossil Record 77***
  - Evolutionary changes within species 77
  - Origins of higher taxa 79
- The Hominin Fossil Record 88***
- Phylogeny and the Fossil Record 91***
- Evolutionary Trends 92***
- Punctuated Equilibria 93***
- Rates of Evolution 96***

## CHAPTER 5

### ***A History of Life on Earth 101***

*Before Life Began 102*

*The Emergence of Life 102*

*Precambrian Life 104*

*Paleozoic Life: The Cambrian Explosion 108*

*Paleozoic Life: Ordovician to Devonian 111*

Marine life 111

Terrestrial life 112

*Paleozoic Life: Carboniferous and Permian 114*

Terrestrial life 114

Aquatic life 115

*Mesozoic Life 115*

Marine life 115

Terrestrial plants and arthropods 116

Vertebrates 119

*The Cenozoic Era 121*

Aquatic life 122

Terrestrial life 123

The adaptive radiation of mammals 123

Pleistocene events 126

## CHAPTER 6

### ***The Geography of Evolution 133***

*Biogeographic Evidence for Evolution 134*

*Major Patterns of Distribution 135*

*Historical Factors Affecting Geographic Distributions 137*

*Testing Hypotheses in Historical Biogeography 140*

Examples of historical biogeographic analyses 141

The composition of regional biotas 145

*Phylogeography 146*

Pleistocene population shifts 146

Modern human origins 147

*Geographic Range Limits: Ecology and Evolution 150*

Range limits: An evolutionary problem 152

*Evolution of Geographic Patterns of Diversity 153*

Community convergence 153

*Effects of History on Contemporary Diversity Patterns 155*

## CHAPTER 7

### ***The Evolution of Biodiversity 161***

*Estimating and Modeling Biological Diversity 162*

Estimates of diversity 162

*Taxonomic Diversity through the Phanerozoic 163*

Rates of origination and extinction 164

Extinction rates have declined over time 165

Do extinction rates change as clades age? 168

Causes of extinction 168

Mass extinctions 169

*Diversification 171*

Modeling rates of change in diversity 171

Does species diversity reach equilibrium? 174

## CHAPTER 8

### ***The Origin of Genetic Variation 187***

*Genes and Genomes 188*

*Gene Mutations 190*

Kinds of mutations 191

Examples of mutations 195

Rates of mutation 196

Phenotypic effects of mutations 200

Effects of mutations on fitness 202

The limits of mutation 205

*Mutation as a Random Process 206*

*Alterations of the Karyotype 207*

Polyploidy 207

Chromosome rearrangements 208

## CHAPTER 9

### ***Variation 215***

*Sources of Phenotypic Variation 217*

*Fundamental Principles of Genetic Variation in Populations 220*

Frequencies of alleles and genotypes: The Hardy-Weinberg principle 221

An example: The human MN locus 223

The significance of the Hardy-Weinberg principle: Factors in evolution 224



- Frequencies of alleles, genotypes, and phenotypes 225
- Inbreeding 225
- Genetic Variation in Natural Populations: Individual Genes 227**
  - Morphology and viability 227
  - Inbreeding depression 229
  - Genetic variation at the molecular level 229
- Genetic Variation in Natural Populations: Multiple Loci 232**
  - Variation in quantitative traits 236
- Variation among Populations 241**
  - Patterns of geographic variation 241
  - Gene flow 244
  - Allele frequency differences among populations 246
  - Human genetic variation 248

## CHAPTER 10

# Genetic Drift: Evolution at Random 255

- The Theory of Genetic Drift 256**
  - Genetic drift as sampling error 256
  - Coalescence 257
  - Random fluctuations in allele frequencies 259
- Evolution by Genetic Drift 260**
  - Effective population size 261
  - Founder effects 263
  - Genetic drift in real populations 263
- The Neutral Theory of Molecular Evolution 266**
  - Principles of the neutral theory 267
  - Variation within and among species 269
  - Support for the neutral theory 270
- Gene Flow and Genetic Drift 272**
  - Gene trees and population history 272
  - The origin of modern *Homo sapiens* revisited 274

## CHAPTER 11

# Natural Selection and Adaptation 279

- Adaptations in Action: Some Examples 280**
- The Nature of Natural Selection 282**
  - Design and mechanism 282
  - Definitions of natural selection 283
  - Natural selection and chance 284
  - Selection of and selection for 284

- Examples of Natural Selection 285**
  - Bacterial populations 285
  - Inversion polymorphism in *Drosophila* 286
  - Male reproductive success 287
  - Population size in flour beetles 288
  - Kin discrimination in cannibalistic salamanders 289
  - Selfish genetic elements 290
- Levels of Selection 290**
  - Selection of organisms and groups 291
  - Species selection 293
- The Nature of Adaptations 294**
  - Definitions of adaptation 294
  - Recognizing adaptations 294
- What Not to Expect of Natural Selection and Adaptation 298**
  - The necessity of adaptation 298
  - Perfection 299
  - Progress 299
  - Harmony and the balance of nature 299
  - Morality and ethics 300

## CHAPTER 12

# The Genetical Theory of Natural Selection 303

- Fitness 304**
  - Modes of selection 304
  - Defining fitness 305
  - Components of fitness 306
- Models of Selection 308**
  - Directional selection 308
  - Deleterious alleles in natural populations 312
- Polymorphism Maintained by Balancing Selection 315**
  - Heterozygote advantage 315
  - Antagonistic and varying selection 317
  - Frequency-dependent selection 318
- Multiple Outcomes of Evolutionary Change 321**
  - Positive frequency-dependent selection 321
  - Heterozygote disadvantage 321
  - Adaptive landscapes 322
  - Interaction of selection and genetic drift 322
- The Strength of Natural Selection 324**
- Molecular Signatures of Natural Selection 325**
  - Theoretical expectations 325
  - Signatures of selection 329
  - Adaptive evolution across the genome 332

## CHAPTER 13

**Phenotypic Evolution 337****Genetic Architecture of Phenotypic Traits 338****Components of Phenotypic Variation 340**

Genetic variance in natural populations 343

**Genetic Drift or Natural Selection? 343****Natural Selection on Quantitative Traits 345**

Response to directional selection 345

Responses to artificial selection 345

Directional selection in natural populations 347

Stabilizing and disruptive selection 348

Evolution observed 348

**What Maintains Genetic Variation in Quantitative Characters? 350****Correlated Evolution of Quantitative Traits 352**

Correlated selection 352

Genetic correlation 352

How genetic correlation affects evolution 354

**Can Genetics Predict Long-Term Evolution? 355****Norms of Reaction 357**

Canalization 357

Phenotypic plasticity 358

Evolution of variability 360

**Genetic Constraints on Evolution 362**

## CHAPTER 14

**The Evolution of Life Histories 369****Individual Selection and Group Selection 371****Modeling Optimal Phenotypes 372****Life History Traits as Components of Fitness 373**

Female fecundity, semelparity, and iteroparity 374

Age structure and reproductive success 376

**Trade-Offs 377****The Evolution of Life History Traits 379**

Life span and senescence 379

Age schedules of reproduction 380

Number and size of offspring 381

**The Evolution of the Rate of Increase 383**

## CHAPTER 15

**Sex and Reproductive Success 387****The Evolution of Mutation Rates 388****Sexual and Asexual Reproduction 388****The Paradox of Sex 389**

Parthenogenesis versus the cost of sex 389

Hypotheses for the advantage of sex and recombination 391

**Sex Ratios and Sex Allocation 393****Inbreeding and Outcrossing 395****The Concept of Sexual Selection 397****Contests between Males and between Sperm 398****Sexual Selection by Mate Choice 400**

Direct benefits of mate choice 400

Indirect benefits of mate choice 402

Sensory bias 405

Antagonistic coevolution 406

**Alternative Mating Strategies 408**

## CHAPTER 16

**Conflict and Cooperation 413****Conflict 414****Social Interactions and Cooperation 417**

Cooperation based on direct benefits 417

Reciprocity: Cooperation based on repeated interactions 418

The evolution of altruism by shared genes 420

**A Genetic Battleground: The Family 424**

Mating systems and parental care 424

Infanticide, abortion, and siblicide 426

Parent-offspring conflict 427

Cooperative breeding 427

Social insects 428

**Genetic Conflict 431****Parasitism, Mutualism, and Levels of Organization 433****Human Behavior and Human Societies 435**

Variation in sexual orientation 435

The question of human nature 437

Cultural evolution and gene-culture coevolution 438



**CHAPTER 17****Species 445****What Are Species? 446**

- Phylogenetic species concepts 447
- The biological species concept 447
- Domain and application of the biological species concept 448
- Taxonomic versus biological species 450
- When species concepts conflict 451

**Barriers to Gene Flow 451**

- Premating barriers 451
- Postmating, prezygotic barriers 453
- Postzygotic barriers 455

**How Species Are Diagnosed 456****Differences among Species 456****The Genetic Basis of Reproductive Barriers 458**

- Genes affecting reproductive isolation 458
- Functions of genes that cause reproductive isolation 461
- Chromosome differences and postzygotic isolation 461
- The significance of genetic studies of reproductive isolation 462

**Molecular Divergence among Species 463****Hybridization 464**

- Primary and secondary hybrid zones 464
- Genetic dynamics in a hybrid zone 465
- The fate of hybrid zones 467

**CHAPTER 18****Speciation 471****Modes of Speciation 472****Allopatric Speciation 473**

- Evidence for allopatric speciation 473
- Mechanisms of vicariant allopatric speciation 476
- Ecological selection and speciation 477
- Sexual selection and speciation 480
- Reinforcement of reproductive isolation 481
- Peripatric speciation 484

**Alternatives to Allopatric Speciation 486**

- Parapatric speciation 486
- Sympatric speciation 487

**Polyploidy and Recombinational Speciation 490**

- Polyploidy 490
- Recombinational speciation 492

**How Fast Is Speciation? 493****Consequences of Speciation 495****CHAPTER 19****Coevolution: Evolving Interactions among Species 499****The Nature of Coevolution 500****Phylogenetic Aspects of Species Associations 501****Coevolution of Enemies and Victims 503**

- Models of enemy-victim coevolution 504
- Examples of predator-prey coevolution 506
- Plants and herbivores 507
- Infectious disease and the evolution of parasite virulence 510

**Mutualisms 513****The Evolution of Competitive Interactions 516**

- Multispecies interactions and community structure 518

**CHAPTER 20****Evolution of Genes and Genomes 523****New Molecules and Processes in Genomes 525****Genome Diversity and Evolution 525**

- Diversity of genome structure 525
- Viral and microbial genomes—the smallest genomes 527
- Repetitive sequences and transposable elements 529
- New genomes reveal major events in the history of life 531

**Protein Evolution and Translational Robustness 532**

- Codon bias 532
- Gene expression and selection on translation errors 533

**Natural Selection across the Genome 534**

- Adaptive molecular evolution in primates 535
- Molecular evolution in the human lineage 536
- Scaling up: From gene to genome 536

**Origin of New Genes 537**

- Lateral gene transfer 537
- Origin of new genes from noncoding regions 537
- Exon shuffling 538
- Gene chimerism 540
- Motif multiplication and exon loss 541

***The Evolution of Multigene Families 542***

Gene duplication 542

Multigene families and the origin of key innovations 543

***Gene and Genome Duplication 545***

Duplication of whole genomes and chromosomal segments 545

Possible fates of duplicate genes 546

Selective fates of recently duplicated loci 548

Rates of gene duplication 549

## CHAPTER 21

***Evolution and Development 553******Hox Genes and the Dawn of Modern EDB 554******Types of Evidence in Contemporary EDB 559******The Evolving Concept of Homology 560******Evolutionarily Conserved Developmental Pathways 563******Gene Regulation: A Keystone of Developmental Evolution 565***

Evolution of protein-coding sequences is also an important contributor to phenotypic evolution 569

Modularity in morphological evolution 569

Co-option and the evolution of novel characters 570

The developmental genetics of heterochrony 571

The evolution of allometry 573

***Developmental Constraints and Morphological Evolution 574******The Molecular Genetic Basis of Gene Regulatory Evolution 578******Toward the EDB of Homo sapiens 581***

## CHAPTER 22

***Macroevolution: Evolution above the Species Level 585******Rates of Evolution 586***

Punctuated equilibrium and stasis 587

***Gradualism and Saltation 590******Phylogenetic Conservatism and Change 592******The Evolution of Novelty 595***

Accounting for incipient and novel features 595

Complex characteristics 597

***Trends and Progress 600***

Trends: Kinds and causes 600

Examples of trends 601

Are there major trends in the history of life? 602

The question of progress 605

## CHAPTER 23

***Evolutionary Science, Creationism, and Society 609******Creationists and Other Skeptics 610******Science, Belief, and Education 611******The Evidence for Evolution 614***

The fossil record 614

Phylogenetic and comparative studies 615

Genes and genomes 615

Biogeography 616

Failures of the argument from design 616

Evolution and its mechanisms, observed 618

***Refuting Creationist Arguments 619***

On arguing for evolution 623

***Why Should We Teach Evolution? 623***

Health and medicine 624

Agriculture and natural resources 627

Environment and conservation 628

Human behavior 629

Understanding nature and humanity 631

***Glossary G-1******Literature Cited LC-1******Index I-1***