

Contents

CHAPTER 1

Evolutionary Biology 1

What Is Evolution? 2

Before Darwin 4

Charles Darwin 5

Darwin's Evolutionary Theory 6

Philosophical Issues 8

Ethics, Religion, and Evolution 9

Evolutionary Theories after Darwin 10

The Evolutionary Synthesis 10

Fundamental principles of evolution 11

Evolutionary Biology since the Synthesis 12

How Evolution Is Studied 13

Evolution as Fact and Theory 15

CHAPTER 2

The Tree of Life: Classification and Phylogeny 19

Classification 21

Inferring Phylogenetic History 25

Phylogenetic trees 25

Data for inferring phylogenies 27

Inferring phylogenies: The method of maximum parsimony 30

Parsimony analysis of DNA sequences: An example 32

Statistical methods of phylogenetic analysis 34

Evaluating phylogenetic hypotheses 37

Estimating Time of Divergence 39

Gene Trees and Species Trees 42

Horizontal gene transfer 42

Incomplete lineage sorting 43

Some Other Aspects of Phylogenetic Analysis 46

Applications and Extensions of Phylogenetics 47

CHAPTER 3

Patterns of Evolution 51

Inferring the History of Character Evolution 52

Some Patterns of Evolutionary Change Inferred from Systematics 53

Most features of organisms have been modified from pre-existing features 55

Homoplasy is common 56

Rates of character evolution differ 60

Evolution is often gradual 61

Change in form is often correlated with change in function 61

Similarity among species changes throughout ontogeny 62

Development and Morphological Evolution 63

Individualization 63

Heterochrony 63

Allometry 64

Heterotopy 66

Increased and decreased complexity 66

Phylogenetic Analysis Documents Evolutionary Trends 67

Many Clades Display Adaptive Radiation 69

Patterns of Evolution in Genes and Genomes 70

Convergent evolution 70

Genome size 71

Duplicated genes and genomes 73

CHAPTER 4

Evolution in the Fossil Record 77

Some Geological Fundamentals 78

Plate tectonics 78

Geological time 79

The geological time scale 79

The Fossil Record 81

Evolutionary changes within species 81

Origins of higher taxa 82

The Hominin Fossil Record 90

- Phylogeny and the Fossil Record* 95
- Evolutionary Trends* 95
- Punctuated Equilibria* 96
- Rates of Evolution* 99

CHAPTER 5

A History of Life on Earth 103

- Patterns in the History of Life* 104
- Before Life Began* 104
- The Emergence of Life* 104
- Precambrian Life* 107
- Paleozoic Life: The Cambrian Explosion* 111
- Paleozoic Life: Ordovician to Devonian* 114
 - Marine life 114
 - Terrestrial life 115
- Paleozoic Life: Carboniferous and Permian* 117
 - Terrestrial life 117
 - The End-Permian mass extinction 118
- Mesozoic Life* 119
 - Marine life 120
 - Terrestrial plants and arthropods 120
 - Vertebrates 122
- The Cenozoic Era* 125
 - Aquatic life 126
 - Terrestrial life 126
 - The adaptive radiation of mammals 126
 - Pleistocene events 129

CHAPTER 6

The Geography of Evolution 135

- Biogeographic Evidence for Evolution* 136
- Major Patterns of Distribution* 137
- Historical Factors Affecting Geographic Distributions* 140
- Testing Hypotheses in Historical Biogeography* 142
 - Examples of historical biogeographic analyses 143
 - The composition of regional biotas 147
- Phylogeography* 148
 - Pleistocene population shifts 149
 - Modern human origins 149

Geographic Range Limits: Ecology and Evolution 152

- Ecological niches 152
- Range limits: An evolutionary problem 154
- Evolution of Geographic Patterns of Diversity* 155
 - Community convergence 155
 - Effects of history on patterns of diversity 157

CHAPTER 7

The Evolution of Biodiversity 161

- Estimating and Modeling Changes in Biological Diversity* 162
 - Modeling rates of change in diversity 162
 - Diversity in the fossil record 163
 - Phylogenetic studies of diversity 164
- Diversity and Disparity through the Phanerozoic* 166
 - Rates of origination and extinction 169
 - Do extinction rates change as clades age? 172
 - Causes of extinction 172
 - Mass extinctions 173
- Diversification* 176
 - Does species diversity reach equilibrium? 176
 - Why are some kinds of organisms more diverse than others? 180
 - Effects of organisms' features on diversification 182
 - Adaptive radiation 183
 - Other influences on diversity 185

CHAPTER 8

The Origin of Genetic Variation 189

- Genes and Genomes* 190
- Mutations: An Overview* 192
 - Kinds of mutations 193
 - Examples of mutations 197
 - Rates of mutation 198
 - Phenotypic effects of mutations 202
 - Effects of mutations on fitness 204
 - The limits of mutation 207
- Mutation as a Random Process* 208
- Alterations of the Karyotype* 209
 - Polyploidy 209
 - Chromosome rearrangements 211

CHAPTER 9

Variation: The Foundation of Evolution 217**Sources of Phenotypic Variation 219**

Genetic and environmental sources of variation 219

Nongenetic inherited variation 221

Understanding Evolution: Fundamental Principles of Genetic Variation 223

Frequencies of alleles and genotypes: The Hardy-Weinberg principle 224

An example: The human *MN* locus 226The significance of the Hardy-Weinberg principle:
Factors in evolution 227

Frequencies of alleles, genotypes, and phenotypes 228

Inbreeding 229

Genetic Variation in Natural Populations: Individual Genes 231

Morphology and viability 231

Inbreeding depression 232

Genetic variation at the molecular level 233

Genetic Variation in Natural Populations: Multiple Loci 235

Linkage and linkage disequilibrium 236

Variation in quantitative traits 239

Variation among Populations 245

Patterns of geographic variation 245

Gene flow 247

Allele frequency differences among populations 248

Human genetic variation 250

CHAPTER 10

Genetic Drift: Evolution at Random 257**Random Processes in Evolution 258****The Theory of Genetic Drift 258**

Genetic drift as sampling error 258

Coalescence 259

Random fluctuations in allele frequencies 261

Evolution by Genetic Drift 263

Effective population size 263

Founder effects 265

Genetic drift in real populations 266

The Neutral Theory of Molecular Evolution 268

Principles of the neutral theory 269

Support for the neutral theory 271

Molecular clocks, revisited 272

Gene Flow and Genetic Drift 273

Gene trees and population history 274

The origin of modern *Homo sapiens* revisited 276

CHAPTER 11

Natural Selection and Adaptation 281**Adaptations in Action: Some Examples 282****The Nature of Natural Selection 284**

Design and mechanism 284

Definitions of natural selection 285

Natural selection and chance 286

Selection of and selection for 287

The effective environment depends on the organism 287

Examples of Natural Selection 288

Experimental evolution 288

Male reproductive success 289

Group selection 290

Kin selection 291

Selfish genetic elements 292

Levels of Selection 292

Selection of organisms and groups 293

Species selection 294

The Nature of Adaptations 296

Definitions of adaptation 296

Recognizing adaptations 297

Adaptive Evolution Observed 301**What Not to Expect of Natural Selection and Adaptation 304**

The necessity of adaptation 304

Perfection 304

Progress 304

Harmony and the balance of nature 305

Morality and ethics 305

CHAPTER 12

The Genetic Theory of Natural Selection 309**Fitness 310**

Modes of selection 310

Defining fitness 312

Components of fitness 313

Models of Selection 315

Directional selection 315

Deleterious alleles in natural populations 319

Polymorphism Maintained by Balancing Selection 322

Heterozygote advantage 322

Antagonistic and varying selection 324

Frequency-dependent selection 325

Multiple Outcomes of Evolutionary Change 328

Positive frequency-dependent selection 328

Heterozygote disadvantage 329

Adaptive landscapes 329

Interaction of Selection and Genetic Drift 330**The Strength of Natural Selection 332****Molecular Evidence for Natural Selection 333**

Detecting selection from geographic variation 333

A test for selection: Variation within and among species 335

Detecting selection from DNA sequences: Theoretical expectations 336

Molecular signatures of selection 339

Adaptive evolution across the human genome 342

Adaptation based on new versus standing variation 343

CHAPTER 13

Phenotypic Evolution 347**Genetic Architecture of Phenotypic Traits 349****Components of Phenotypic Variation 351****Evolution of Quantitative Traits by Genetic Drift 354****Selection on Quantitative Traits 355**

Response to directional selection 355

Responses to artificial selection 356

Directional selection in natural populations 357

Stabilizing and disruptive selection 359

Correlated Evolution of Quantitative Traits 360

Correlated selection 360

Genetic correlation 361

How genetic correlation affects evolution 362

Can Genetics Predict Long-Term Evolution? 363**Norms of Reaction 366**

Canalization 366

Phenotypic plasticity 367

Evolution of variability 368

Adaptation and Constraint 372

Genetic constraints on adaptation 372

Can adaptation rescue species from extinction? 373

CHAPTER 14

The Evolution of Life Histories 379**Individual Selection and Group Selection 381****Modeling Optimal Phenotypes 382****Life History Traits as Components of Fitness 384**

Fecundity, semelparity, and iteroparity 384

Age structure and reproductive success 386

Trade-Offs 387**The Evolution of Life History Traits 389**

Life span and senescence 389

Age schedules of reproduction 390

Number and size of offspring 393

Life Histories and Mating Strategies 394**Evolution of the Rate of Increase 395**

CHAPTER 15

Sex and Reproductive Success 399**The Evolution of Mutation Rates 400****Sexual and Asexual Reproduction 401****The Paradox of Sex 401**

Benefits and costs of recombination and sex 401

Hypotheses for the advantage of sex and recombination 403

Sex Ratios and Sex Allocation 406**Inbreeding and Outcrossing 409****The Concept of Sexual Selection 411****Contests between Males and between Sperm 412****Sexual Selection by Mate Choice 414**

Direct benefits of mate choice 414

Mate choice without direct benefits 415

Variations on the theme of sexual selection 420

CHAPTER 16

Conflict and Cooperation 427**Modelling Conflict 428****Social Interactions and Cooperation 430**

- Cooperation among unrelated individuals 431
- The evolution of altruism by means of shared genes 434

**An Arena for Cooperation and Conflict:
The Family 438**

- Mating systems and parental care 438
- Infanticide, abortion, sibling competition, and siblicide 440
- Parent-offspring conflict 441
- Eusociality 442

Kin Selection or Group Selection? 444**Genetic Conflict 445**

- Cytoplasmic inheritance 446
- Meiotic drive 446
- Post-segregation distorters 447
- Transposable elements 448
- Conflict between parental genomes 448

**Parasites, Mutualists, Individuals, and Levels of
Organization 449****Human Behavior and Human Societies 450**

- Evolutionary approaches to human behavior 451
- Cultural evolution and gene-culture coevolution 454

CHAPTER 17

Species 459**What Are Species? 460**

- Phylogenetic species concepts 461
- The biological species concept 461
- Domain and application of the biological species concept 463

Barriers to Gene Flow 464

- Premating barriers 465
- Postmating, prezygotic barriers 468
- Postzygotic barriers 468
- Multiple isolating barriers 469

How Species Are Diagnosed 469**Differences among Species 470****The Genetic Basis of Reproductive Isolation 472**

- Chromosome differences and postzygotic isolation 472
- Genes affecting reproductive isolation 473

The significance of genetic studies of reproductive isolation 476

Genetic Divergence and Exchange 476

- Ancestral variation and coalescence 476
- Gene flow and hybridization 478
- The fate of hybrid zones 481

CHAPTER 18

Speciation 483**Modes of Speciation 484****Allopatric Speciation 485**

- Evidence for allopatric speciation 486
- Mechanisms of vicariant allopatric speciation 488
- Ecological selection and speciation 489
- Sexual selection and speciation 492
- Reinforcement of reproductive isolation 494
- Peripatric speciation 496

**Alternatives to Allopatric Speciation: Speciation with
Gene Flow 499**

- Genomic studies of speciation with gene flow 500
- Parapatric speciation 501
- Sympatric speciation 502

Polyploidy and Recombinational Speciation 505

- Polyploidy 505
- Recombinational speciation 507

How Fast Is Speciation? 508**Consequences of Speciation 509**

CHAPTER 19

**The Evolution of Interactions
among Species 513****Interactions among Species 514**

- Coevolution 515
- Phylogenetic aspects of species associations 515

Coevolution of Enemies and Victims 517

- Models of enemy-victim coevolution 518
- Examples of predator-prey evolution 519
- Aposematism and mimicry 521
- Plants and herbivores 522
- Parasite-host interactions and infectious disease 525

Mutualisms 529

The Evolution of Competitive Interactions 531
Evolution and Community Structure 534

CHAPTER 20

Evolution of Genes and Genomes 537

Diverse Players and Evolutionary Processes in Genomes 539

Nonadaptive Processes in Genome Evolution 541

Rates and Patterns of Protein Evolution 542

Codon bias 542

Gene dispensability and selection for translational robustness 543

Protein interactions and rates of evolution 544

Developmental biology and rates of protein evolution 545

Genome Diversity and Evolution 546

Diversity of genome structure 546

Viral and microbial genomes: The smallest genomes 547

Repetitive sequences and transposable elements 548

Natural Selection Across the Genome 550

Molecular convergence as evidence for natural selection 551

Molecular evolution in the human lineage 553

Origin of New Genes 554

Horizontal gene transfer 554

Exon shuffling, protein domain evolution, and chimerism 555

Gene Duplication 556

The fates of duplicate genes 557

Ohno's dilemma, molecular promiscuity, and the selective fates of recently duplicated loci 558

Multigene families and the origin of key innovations 560

Genome and Chromosome Duplication 562

CHAPTER 21

Evolution and Development 565

Hox Genes and the Dawn of Modern EDB 566

Evolution of Hox gene expression and function 570

New concepts of homology 571

Evidence of Developmental Evolution Underlying Morphological Evolution 572

Evolutionarily Conserved Developmental Pathways 575

Gene Regulation: A Keystone of Developmental Evolution 578

Protein-Coding Sequences and Phenotypic Evolution 582

The Molecular Genetic Basis of Gene Regulatory Evolution 583

Modularity in morphological evolution 585

Macroevolution and the evolution of novel characters 586

The Evolution of Morphological Form 589

The developmental genetics of heterochrony 590

The evolution of allometry 593

Developmental Constraints and Morphological Evolution 594

Character Loss, Reversal, and Dollo's Law 596

Ecological Developmental Biology 597

Evolution of Human Development 600

CHAPTER 22

Macroevolution: Evolution above the Species Level 605

Rates of Evolution 606

Gradualism and Saltation 609

Phylogenetic Conservatism and Change 611

The Evolution of Novelty 614

Accounting for incipient and novel features 614

Complex characteristics 615

Trends, Predictability, and Progress 620

Trends: Kinds and causes 621

Examples of trends 621

Are there major trends in the history of life? 623

Predictability and contingency in evolution 626

The question of progress 628

CHAPTER 23

Evolutionary Science, Creationism, and Society 631

Creationists and Other Skeptics 632

Science, Belief, and Education 634

The nature of science 634

Evolution as fact and as theory 635

The Evidence for Evolution 636

The fossil record 637

Phylogenetic and comparative studies 637

Genes and genomes 638

Biogeography 638

Failures of the argument from design 639

Evolution, and its mechanisms, observed 640

Refuting Creationist Arguments 641

On arguing for evolution 645

Why Should We Teach Evolution? 646

Health and medicine 647

Agriculture and natural resources 650

Environment and conservation 651

Human behavior 652

Understanding nature and humanity 654

Glossary G–1***Literature Cited LC–1******Illustration Credits IC–1******Index I–1***