

Contents

List of Figures	xvii
List of Tables	xxiii
List of Foundations	xxiv

Part 1 Introduction	1
----------------------------	----------

1 Evolutionary Cell Biology	3
------------------------------------	----------

The Dominance of Unicellular Life	4
What is Evolutionary Cell Biology?	5
The Completeness of Evolutionary Theory	7
Evolution Via Nonadaptive Pathways	10
The Grand Challenges	11
The origin of life	11
The roots of organismal complexity	12
Molecular stochasticity	12
Molecular complexes	13
Cellular networks	13
Cellular surveillance systems	13
Growth regulation	14
Biological scaling laws	14

2 The Origin of Cells	18
------------------------------	-----------

The Earliest Stages	19
The alkaline hydrothermal-vent hypothesis	22
The terrestrial geothermal-field hypothesis	24
An Early RNA World?	25
Membranes and the Emergence of Individuality	27
Genomic Constraints on the Establishment of Life	30

3 The Major Lines of Descent	45
-------------------------------------	-----------

The Primary Domains of Life	46
Times of Origin	49
The Emergence of Eukaryotes	50

The stem eukaryote	50
The eukaryotic radiation	52
A eukaryotic Big Bang?	53

Part 2 The Genetic Mechanisms of Evolution **61**

4 The Population-Genetic Environment **63**

Demystifying Random Genetic Drift	63
The Genetic Effective Sizes of Populations	67
Probability of Fixation of a Mutant Allele	68
Evolution of the Mutation Rate	70
High mutability of mutation rates	73
Error-prone polymerases	73
Optimizing the mutation rate	74
The non-random nature of mutation	75
Recombination	76
Evolution of the recombination rate	80

5 Evolution as a Population-Genetic Process **91**

The Perils of the Adaptive Paradigm	92
The Fitness Effects of New Mutations	92
The Classical Model of Sequential Fixation	95
Vaulting Barriers to More Complex Adaptations	98
Sequential fixation versus stochastic tunnelling	99
Two-locus transitions	101
More complex scenarios	102
Effects of recombination	104
The Phylogenetic Dispersion of Mean Phenotypes	105
Two-state traits	105
Multistate-traits and the drift-barrier hypothesis	106

6 Evolution of Cellular Complexity **118**

Illusions of Grandeur	118
Constructive Neutral Evolution	120
Ribosomes	122
Evolution by Gene Duplication	124
The masking effect	126
Neofunctionalization	126
Subfunctionalization	126
Adaptive-conflict resolution	128
The Case for Subfunctionalization	128
The Emergence of Modular Gene Subfunctions	131
The Passive Origin of Species via Gene Duplication	133

Part 3 Basic Cellular Features	143
7 The Cellular Environment	145
The Molecular Composition of Cells	145
Water	146
Elemental composition	146
Biomolecules	149
Numbers of Biomolecules per Cell	149
Passive Transport of Particles through the Cytoplasm	152
Intermolecular Encounter Rates	155
Temperature-Dependence of Biological Processes	156
Energy, Carbon Skeletons, and Cell Yield	158
8 Evolutionary Scaling Relationships in Cell Biology	168
Describing Allometric Relationships	169
Scaling Laws in Cellular Bioenergetics	170
Metabolic rate	170
Lifetime energy requirements of a cell	171
The speed limit on cell-division rates	174
The Limits to Natural Selection Imposed by the Drift Barrier	177
Membrane Bioenergetics and the Prokaryote–Eukaryote Transition	180
Energy production and the mitochondrion	181
Cellular investment in ribosomes	183
The mitochondrion as a driver of eukaryotic evolution	183
9 Cell Growth and Division	191
Ribosomes and Cell Growth	191
Models for Cellular Growth	194
Control of Cell Size	196
Molecular mechanisms of division-size determination	198
Environmental determinants of cell size	201
Scaling of Intracellular Features	203
Phenotypic Variation in Cell Size and Division Time	205
Stochastic partitioning of cell contents at division	206
Phenotypic Variation and Adaptation	208
Environmental variation and the efficiency of selection	208
Inheritance of environmental effects	210
The adaptive value of phenotypic variation	211
10 The Cell Life Cycle	225
The Eukaryotic Cell Cycle	226
Phylogenetic diversity	227
Network complexity	229

17 The Costs of Cellular Features **411**

The Bioenergetic Cost of a Cellular Feature	411
The Evolutionary Cost of a Cellular Feature	414
Biosynthetic Costs of Nucleotides and Amino Acids	415
An Empirical Shortcut to Cost Estimates	417
The Energetic Cost of a Gene	419
Chromosome-associated costs	420
Transcription-associated costs	421
Translation-associated costs	423
Evolutionary implications	424
The Cost of Lipids and Membranes	427
Costs of individual molecules	428
Total cellular investment	428

18 Resource Acquisition and Homeostasis **443**

Adaptive Fine-Tuning of Elemental Composition	443
Nutrient Uptake Kinetics	445
Channels and transporters	446
Physiological acclimation	448
Advantages of motility	448
Photosynthesis	450
The transformation of solar to chemical energy	451
The world's most abundant enzyme	452
Osmoregulation	455
Circadian Rhythms	457

19 Enzymes and Metabolic Pathways **470**

Enzymes	471
Basic enzymology	471
Degree of molecular perfection	472
Enzyme promiscuity	475
Pathway Flux Control	476
Pathway position and the strength of selection	476
Speed versus efficiency	478
Pathway Expansion and Contraction	479
Stochastic meandering of pathway architecture	480
The origin of novel enzymes	483
Pathway Participant Remodelling	484
Non-orthologous gene replacement	487
Internal pathway expansion via multifunctional enzymes	489

20 Intracellular Errors	505
--------------------------------	------------

Transcript Fidelity	506
Translational Fidelity	509
Biophysics of Substrate Discrimination and the Cost of Proof-Reading	511
The Limits to Selection on Error Rates	513
The Evolutionary Consequences of Surveillance-Mechanism Layering	515
Adaptive Significance of Errors	517

21 Transcription	531
-------------------------	------------

Molecular Stochasticity in Single Cells	532
Cellular mRNA abundances	532
Cellular protein abundances	535
Expression noise and adaptation	536
The Basic Biology of Transcription	538
A physical model for TF binding	538
Encounter rates between TFs and their binding sites	540
Coevolution of Transcription Factors and Their Binding Sites	541
General observations	542
Evolutionary distributions of binding site motifs	543
Application of the models	545
Evolution of Pathway Architecture	547
Activators versus suppressors	548
Regulatory rewiring	549
Network topology	551

22 Environmental Sensing	570
---------------------------------	------------

Bacterial Signal Transduction Systems	571
Origin and diversification	572
Coevolutionary integration of components	574
Emergence of new pathways	575
Interconvertible Proteins and Ultrasensitivity	577
The cost of signal transduction	580
Similarities and differences in eukaryotic systems	580
Chemotaxis	583
Accuracy of environmental assessment	586
Phenotypic Bimodality and Bet-Hedging	587
Adaptive fine-tuning versus inadvertent by-products of pathway structure	588

Part 7 Organismal Complexity **601**

23 Endosymbiosis **603**

Mitochondria	604
Origins	604
Energetic boost or burden	607
Functional remodelling	609
The Extreme Population-Genetic Environments of Mitochondria	610
Mutation rates	611
Modes of inheritance	612
Muller's ratchet	614
Organelle Genome Degradation	615
Animal mitochondrial tRNAs	616
Coevolutionary drive and compensatory mutations	617
Plastid Evolution	618
Addiction to Endosymbionts	620

24 Origins of Organismal Complexity **636**

Deconstructing the Great Chain of Being	637
Genome complexity and organismal complexity	639
A shake-up of genomic organization in the ancestral eukaryote	640
Multicellularity	642
Multicellularity and cooperativity in bacteria	643
The costs of multicellularity	645
The emergence of cell type specialization	647
Closing Comments	649

Index **655**