



Contents

Preface	x
PART I Foundations	3
1 Introduction	4
1.1 From Darwin to Development	4
1.2 Development; and Evolutionary Changes in Development	9
1.3 Development and the Realm of Multicellularity	11
2 What is Evo-Devo?	15
2.1 Forerunners of Evo-Devo	15
2.2 Nineteenth-Century Comparative Embryology	16
2.3 Diverse Antecedents—1900–1980	19
2.4 Conclusions from History; Messages for the Present	24
2.5 The Advent of Evo-Devo in the 1980s	25
2.6 Broad and Narrow Views of Evo-Devo	27
2.7 Too Few Laws, Too Many Facts?	28
3 Development, Cells and Molecules	34
3.1 Analysing the Developing Organism	34
3.2 Cells and Development: The Basics	37
3.3 Genes: Structure, Expression and Developmental Function	40
3.4 Signalling Pathways Within and Between Cells	45
3.5 Signalling: From Cell to Embryo	48
3.6 Long-Range Signalling and Developmental Processes	51
4 Natural Populations	54
4.1 The Ecological Theatre and the Evolutionary Play	54
4.2 Types of Creature: Types of Population	55
4.3 Spatial Structure	60
4.4 Age Structure	64
4.5 Genetic Structure	65
4.6 Natural Selection	67

PART II Developmental Repatterning	75
5 Mutation and Developmental Repatterning	77
5.1 Mutation in Terms of Altered DNA Sequence	77
5.2 Mutation in Terms of Proximate Functional Consequences	80
5.3 Developmental Repatterning at Molecular and Higher Levels	82
5.4 Developmental Repatterning at the Level of the Whole Organism	88
5.5 Developmental Repatterning and Fitness	89
6 Heterochrony	93
6.1 What is Heterochrony?	93
6.2 Types and Levels of Heterochrony	94
6.3 Heterochrony at the Organismic Level	95
6.4 Heterochrony at the Molecular Level	99
6.5 Heterochrony and Fitness	102
7 Heterotopy	106
7.1 What is Heterotopy?	106
7.2 Heterotopic Processes Involving Left-Right Asymmetry	107
7.3 Heterotopic Processes Involving the A-P and D-V Axes	112
7.4 Other Types of Heterotopy	116
7.5 Concluding Remarks	119
8 Heterometry	121
8.1 What is Heterometry?	121
8.2 Increasing Relative Size	122
8.3 Decreasing Relative Size	124
8.4 Bi-directional Heterometry	128
8.5 Heterometric Compensation	132
9 Heterotypy	135
9.1 What is Heterotypy?	135
9.2 Altered Products of Developmental Genes	137
9.3 Altered Pigmentation	139
9.4 Altered Morphology and the Origin of Novelty	140
9.5 The Origin of New Cell Types	144
10 The Integrative Nature of Repatterning	148
10.1 Repatterning is a Complex Process	148
10.2 Different Kinds of Repatterning can Produce a Similar Result	149
10.3 Compound Repatterning at a Single Level of Organisation	151
10.4 The Kind of Repatterning can Change Between Levels of Organisation	155

10.5 Categories and Subcategories of Repatterning	157
10.6 The Causes of Repatterning	159
11 Mapping Repatterning to Trees	161
11.1 Pattern, Process, Homology and Trees	161
11.2 The Origin(s) of Animal Segmentation	163
11.3 The Vertebrate Fin-to-Limb Transition	169
11.4 The Origin of Flowers	176
11.5 General Conclusions on Repatterning and Selection	179
PART III The Direction of Evolution	183
12 Adaptation, Coadaptation and Exaptation	185
12.1 Natural Selection on a Continuously Variable Character	185
12.2 Natural Selection on Two Characters; and the Idea of an Adaptive Landscape	190
12.3 Developmental and Functional Coadaptation	191
12.4 Morphological Geometry and Selection	194
12.5 Long-term Evolution and Exaptation	196
13 Developmental Bias and Constraint	200
13.1 A Key Question about Evolution's Direction	200
13.2 Making Sure the Question is about Processes, not Terminology	204
13.3 Dependence versus Independence of Different Characters	208
13.4 Evo-Devo Meets Quantitative Genetics	209
13.5 Developmental Bias and 'Routine' Evolution	211
13.6 Developmental Bias and the Origin of Evolutionary Novelty	216
14 Developmental Genes and Evolution	218
14.1 The Direction of Evolution at the Developmental/Genetic Level	218
14.2 Developmental Genes: An Overview	219
14.3 Developmental Genes: Examples	223
14.4 The Hox Genes	225
14.5 Gene-Level Forms of Developmental Bias and Coadaptation	230
14.6 Changes in Regulatory versus Coding Regions of Genes	231
15 Gene Co-option as an Evolutionary Mechanism	234
15.1 What is Gene Co-option?	234
15.2 Co-option in the Evolution of Segments and Eyes	237
15.3 Appendage Evolution and Gene Co-option	241
15.4 Co-option in the Evolution of Zygomorphic Flowers	244
15.5 Evolution of the 'Genetic Toolkit'	245
15.6 Co-option, Exaptation and Developmental Bias	249
16 Developmental Plasticity and Evolution	252
16.1 Types of Developmental Plasticity	252
16.2 Discrete Variants: Winged and Wingless Forms of Insects	254

16.3 Meristic Variation: the Number of Segments in Centipedes	257
16.4 Continuous Variation: Plant Growth	259
16.5 Plasticity and Developmental Genes	260
16.6 The Evolution of Patterns of Plasticity	261
17 The Origin of Species, Novelities and Body Plans	272
17.1 Is Evolution Scale-dependent?	272
17.2 Speciation	273
17.3 The Origin of Novelities	281
17.4 Body Plans I: Overview	284
17.5 Body Plans II: the Origin of the Vertebrates	285
17.6 Body Plans III: the 'Cambrian Explosion'	286
18 The Evolution of Complexity	291
18.1 Defining Complexity	291
18.2 The Lack of a 'Law of Increasing Complexity'	293
18.3 Increases in the Complexity of Adults	299
18.4 Changes in the Complexity of Life-histories	302
18.5 Complexity at the Molecular Level	306
PART IV Conclusions	311
19 Key Concepts and Connections	312
19.1 Introduction: From Original Idea to Mature Scientific Discipline	312
19.2 A List of The Book's Main Points, and the Emergence of Key Concepts	314
19.3 How do They Inter-Connect?	319
20 Prospects	327
20.1 Introduction: From the Present into the Future	327
20.2 Molecular Evo-Devo	327
20.3 Integrative Evo-Devo and General Evolutionary Theory	332
20.4 Wider Challenges	334
Glossary	336
Appendix 1: A Little Bit of History	355
Appendix 2: Naming of Genes and Proteins	359
Appendix 3: Geological Time	363
Appendix 4: Inferring Evolutionary Trees from Comparative Data	366
References	370
Index	383

This book has a companion website: www.wiley.com/go/arthur/evolution