

# EPIGENETIC PRINCIPLES OF EVOLUTION

SECOND EDITION

NELSON R. CABEJ

*Epigenetic Principles of Evolution*, Second Edition, fully examines the causal basis of evolution from an epigenetic point of view. By revealing the epigenetic “user” of the “genetic toolkit,” this work demonstrates the primacy of epigenetic mechanisms and epigenetic information in generating evolutionary novelties.

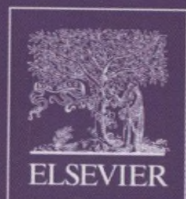
The author convincingly supports his theoretical perspective with a host of examples from varied fields of biology, emphasizing changes in developmental pathways as the basic source of evolutionary change in metazoans. The book therefore provides a broader view of epigenetic mechanisms of evolution, moving beyond conventional changes in epigenetic structures such as DNA methylation, histone modifications, and patterns of miRNA, sRNA, and mRNA expression.

This second edition is thoroughly updated to reflect new evidence, as well as developing theories in the field of evolutionary epigenetics. New and revised chapters speak to the epigenetic basis of heredity, epigenetic regulation of animal structure and homeostasis, neural manipulation of gene expression, central control of gametogenesis, epigenetic control of early development, the origin of epigenetic information, evolutionary changes in response to environmental stressors, epigenetics of sympatric evolution, and epigenetics of the Cambrian explosion among other topics.

## Key Features

- Adopts an integrative approach to examine the causal basis of evolution from an epigenetic point of view, with the aim of overcoming current difficulties in the theory of evolution
- Features all new and revised chapters, which reflect novel experimental and observational evidence in the field of evolutionary epigenetics, as well as alternative theoretical approaches
- Offers a broad view of epigenetic mechanisms of evolution, moving beyond conventional changes in epigenetic mechanisms such as DNA methylation, histone modifications, and patterns of miRNA, sRNA, and mRNA expression

GENETICS



ACADEMIC PRESS

An imprint of Elsevier  
[elsevier.com/books-and-journals](http://elsevier.com/books-and-journals)

ISBN 978-0-12-814067-3



9 780128 140673



## Part I

# Epigenetic Basis of Metazoan Inheritance

1. Control Systems and Determination of Phenotypic Traits in Metazoans	3
The Thermodynamic Enigma of Living Systems	3
On the Meaning of Biological Information—Genetic vs Epigenetic Information	4
Novel Properties of the Biological Information	6
The Control System in Living Beings and the von Neumann's Machine	7
Central Control of Animal Physiology	10
Neural Control of Water Content	11
Neural Control of Glucose and Insulin Biosynthesis	11
Neural Control of Thermoregulation	14
Central Control of Animal Behavior	17
Neural Control of Locomotion	17
Neural Determination of Monogamy in Prairie Voles	18
Central Control of Metazoan Morphology	18
Control of Expression of Nonhousekeeping Genes	19
Chromatin Remodeling in Control of Gene Expression	20
DNA Methylation and Gene Expression	22
Hormonal Control of Secreted Proteins and Growth Factors	25
Neural Control of the Endocrine Function	26
Examples of Central Control of Metazoan Morphology	29
Development of the Mammary Gland	29
Central Determination of Body Mass	31
The Integrated Control System	31
The Hypothesis of the Epigenetic System of Heredity and Its Predictions	32
References	33
Further Reading	39



<b>2. Neural Manipulation of Gene Expression</b>	<b>41</b>
Predetermined vs Manipulative Expression of Genes	41
Processing of External/Internal Stimuli in the CNS Generates Information for Adaptive Phenotypic Responses	43
Epigenetic Manipulation of Genetic Information in the CNS	51
Epigenetic Information Is Generated in Neural Circuits	54
Neural Processing of Stimuli Generates Information for Postphylogenetic Development	59
What Do Neural Circuits Do: Sum up Stimuli or Figure out Adaptive Responses?	64
References	67
Further Reading	73
<b>3. Epigenetic Control of Reproduction</b>	<b>75</b>
Epigenetic Control of Reproductive Physiology and Behavior	75
Neuroendocrine Regulation of the Reproduction and Gonadal Function in Insects	75
Local Neural Control of the Reproductive Function in Insects	79
Neuroendocrine Regulation of Reproductive Function in Vertebrates	80
Local Neural Control of the Reproductive Function in Vertebrates	82
Epigenetic Control of Gametogenesis	83
Neural Control of Oogenesis in Insects and Gastropod Molluscs	83
Neural Control of Oogenesis in Vertebrates	84
Neuroendocrine Control via the Brain-Hypothalamic-Pituitary Axis	84
Local Control by Ovarian Innervation	86
Neural Control of Spermato-/Spermiogenesis	87
Neural Control of Deposition of Parental Epigenetic Information in Gametes	88
Neural Control of Deposition of Maternal Factors in Insect Oocytes	89
Neural Control of the Squeezing of Nurse Cell Content into the Oocyte	90
Microtubules are Involved in Transportation and Placement of Maternal Factors in the Oocyte	93
Neurohormonal Regulation of Length of Microtubules	94
The Nervous System Manipulates the Length and Orientation of Microtubules	96
Other Modes of Neural Control of Deposition of Parental Epigenetic Information in Vertebrate Eggs	97
Neural Regulation by Modifying Maternal Hormone Level	97
Neural Regulation by Differential Uptake from the Blood	99
Regulation via Intercellular Communication Channels	100
Role of the Ovarian Innervation in the Ovarian Function	101
Paternal Cytoplasmic Factors in the Sperm Cell	102
Neural Control of Gene Imprinting	103
References	105
Further Reading	116



<b>4. Epigenetic Control of Early Development</b>	<b>119</b>
Epigenetic Control of Formation of Primordial Germ Cells	119
Epigenetic Control of Migration of PGCs	121
Epigenetic Control of Early Development in Insects	122
Epigenetic Control of Early Development in Vertebrates	123
Epigenetic Control of Early Development in Mammals	124
Epigenetic Control of Formation of Embryonic Germ Layers	128
Maternal Control of Endoderm Formation	128
Maternal Control of Mesoderm Formation	129
Epigenetic Control of Neural Induction and Formation of the CNS	129
References	129
Further Reading	132
	136

<b>5. Neural Control of Postphylotypic Development</b>	<b>137</b>
Neural Control of Postphylotypic Development	137
Neural Control of Metamorphosis	138
Apoptosis in Invertebrates	138
Postphylotypic Development	146
The Embryonic Central Nervous System Controls the Postphylotypic	146
Left-Right Asymmetry	157
Neural Control of the Development of the Neuroendocrine System	159
The Pituitary	159
The Adrenal Gland	160
The Pancreas	160
The Thymus	161
Neural Control of the Development of Sensory Organs	162
Inner Ear	162
Maternal and Neural Control of Heart Development	163
Vasculogenesis and Angiogenesis	165
Development of the Submandibular Gland	166
Development of the Gastrointestinal Tract	168
Vertebrate Head	168
Pneumogenesis	169
Nephrogenesis	173
Neural Control of the Primary Sex Determination	175
Neural Control of Sex Conversion	176
Osteogenesis	178
Regulation of Bone Homeostasis	180
Immediate Neural Regulation of Bone Homeostasis	182
Neural Control of the Development of the Mammary Gland	183
Neural Control of the Development of Body Mass	184
Neural Control of the Lifespan in Invertebrates	187
Neural Control of the Onset of Puberty	189
Neural Control of Apoptosis	190



Neural Control of Regeneration	194
Local Control of Regeneration by Nerve Fibers	194
Neurohormonal Control of Regeneration by the Nervous System	198
References	199
Further Reading	213
<b>6. The Epigenetic System of Inheritance</b>	<b>215</b>
The Epigenetic System of Inheritance	216
Gametogenesis and Provision of Maternal Epigenetic Information to Oocytes	218
Biphasic CNS Control of Reproduction	224
The Parental CNS-Controlled Phase of Reproduction: Formation of Bauplan and the CNS	225
The Embryonic CNS-Controlled Phase: The Phylotypic Development	228
The Binary Neural Control of Gene Expression	230
Spatial Restriction of Gene Expression	233
The Epigenetic System of Inheritance and the Evolution of Animals	235
Inheritance of Acquired Traits	236
Empirical Evidence on Inheritance of Acquired Behavioral and Life History Traits	236
Empirical Evidence of Inheritance of Acquired Morphological Traits	237
Emergence of Acquired Traits	241
Transmission of Acquired Traits	244
Novel Features of the Epigenetic System of Inheritance	246
References	251
Further Reading	258
<b>7. Adaptation to Changed Conditions of Living and Evolution</b>	<b>259</b>
Adaptation to Changed Conditions of Living	259
Neural Basis of Innate Behavior	260
Neural Basis of Learned Behavior	268
Animal Behavior Is Not Determined by Genes	271
Learned Behaviors Evolve into Innate Behaviors	275
Behavioral Atavisms—Activation of Ancestral Behavioral Circuitries	279
Developmental and Evolutionary Relationship Between Behavior and Morphology	282
References	288
Further Reading	292



## Part II

# Epigenetics of Circumevolutionary Phenomena and the Mechanism of the Evolutionary Change

8. Intragenerational Developmental Plasticity	295
Developmental Plasticity: Beyond the Reaction Norm	295
Developmental Plasticity and Possible Evolutionary Implications	299
Adaptive Intragenerational Developmental Plasticity	300
Camouflage (Adaptive Coloration, Cryptic Coloration, Crypsis)	300
Polyphenisms in Invertebrates	308
How Did the Divergence in the Body Color Evolve?	312
Seasonal Polyphenism in Insects	313
Neo-Darwinian Explanation of the Seasonal Polyphenisms in Insects	316
Epigenetic Explanation of Seasonal Polyphenisms in Insects	317
Experimental Polyphenisms in Insects	320
Polyphenisms in Vertebrates	321
Experimental Polyphenisms in Vertebrates	324
Predator-Induced Defenses	325
Inborn Developmental Plasticity	327
Developmental Polymorphisms Are Not Genetic Polymorphisms	327
References	329
Further Reading	336
9. Transgenerational Developmental Plasticity— An Epitome of Evolutionary Change	337
Transgenerational Developmental Plasticity—Inherited Changes Without Changes in Genes	338
Transgenerational Developmental Plasticity in Nature	338
Phase Transition in Locusts	344
Transgenerational Developmental Plasticity in Experiments	349
Reconstructing the Chain of Events in Transgenerational Plasticity	354
The Mechanism of Induction of Sexually Reproducing Generation in <i>Daphnia magna</i>	354
Insect Diapause	356
Diapause in the Silkworm	356
A Neurotransmitter Coding for a Life History Character	357
The Mechanism of Transgenerational Phase Transition in Locusts	359
The Origin of the Information for Transgenerational Developmental Plasticity	363
References	369
Further Reading	374



## Part III

# Epigenetics of Metazoan Evolution

10. Origins of Evolutionary Novelty	379
The Epigenetic Hypothesis of Evolution and Its Predictions	379
The Nature of the Evolutionary Change	381
Interactions Organism-Environment in Evolution: The Causal Relationship	382
Behavioral Prelude of Evolutionary Modifications of Animal Morphology	388
Evolution of Morphology/Morphometry	390
Evolution of Body Size in <i>Manduca sexta</i>	392
The Growth Rate	393
Critical Weight	393
PTTH Delay Time	394
Evolution of Wings in Insects	395
Neural Control of Developmental Pathways and Gene Regulatory Networks of Insect Wings	397
Evolution of Caste Developmental Polymorphisms in Insects	402
Neo-Darwinian Explanation	408
Epigenetic Explanation	409
Evolution of the Seasonal Diphenism in the Butterfly <i>Bicyclus anynana</i>	409
Neo-Darwinian Explanation	410
Epigenetic Explanation	411
Evolution of Horns in Beetles	411
Neo-Darwinian Explanation	414
Epigenetic Explanation	415
Evolution of Appendages and Tetrapod Limbs	416
Role of the Nervous System in Limb Development	416
Evolution of Wings in Bats	423
Neo-Darwinian Explanation	424
Epigenetic Explanation	425
Evolution of Blood Circulatory System	426
Evolution of Air Breathing Surfactant System in Vertebrates	426
Neo-Darwinian Explanation	428
Epigenetic Explanation	429
Evolution of Dentition in Vertebrates	429
Role of the Nervous System in Teeth Development	430
Neo-Darwinian Explanation	435
Epigenetic Explanation	435
Sudden Evolution of Morphology in the Threespine Stickleback, <i>Gasterosteus aculeatus</i>	436
Evolution of the Auditory System	436
Evolution of Ears and Ultrasonic Echolocation in Insects	438
Evolution of Ears in Vertebrates	439
Neo-Darwinian Explanation	441



Epigenetic Explanation	441
Evolution of Eyes	441
Evolution of Feathers	443
Molecular Mechanism of Feather Development	443
Successive Stages in Evolution of Feathers	445
Neo-Darwinian Explanation	446
Epigenetic Explanation	446
Evolution of Sexual Dichromatism in Birds	446
Neo-Darwinian Explanation	447
Epigenetic Explanation	449
Evolution of Life Histories	452
Evolution of Sexual Reproduction and Alternation of Asexual and Sexual Modes of Reproduction	452
Neo-Darwinian Explanation	456
Epigenetic Explanation	456
Evolution of Pedomorphosis in a Salamander Species	458
Evolution of Viviparity	460
Neo-Darwinian Explanation	465
Epigenetic Explanation	465
Evolution of Behavioral Characters in Insects	466
Evolution of Flight in Insects	466
Evolution of Avoidance Behavior in the Green Tree- and Red-Bellied Snakes	467
Evolution of a New Ovulation Character in House Finches	470
Evolution of the Circadian System in Blind Moles	470
Neural Mechanisms of Metazoan Migration	471
Light-Dependent Magnetic Orientation	471
Trigeminal System of Geomagnetic Orientation	473
Experimental Induction and Evolution of New Characters	475
Rapid Evolution of Physiological Characters in <i>Drosophila</i>	475
Neo-Darwinian Explanation	475
Epigenetic Explanation	475
References	476
Further Reading	491

<b>11. Evolution by Loss</b>	<b>493</b>
Vestigialization of Metazoan Structures	493
Vestigialization of Limbs in Squamates	494
Simplification of the Brain and Morphology in Plethodontid Salamanders	495
Loss of Animal Structures in Nature	495
Loss of Wings in Insects	496
Loss of Wings in Phasmids	496
Loss of the Gas Bladder in Fish	497
Loss of Teeth in Birds	497
Loss of Teeth in Whales	499
Loss of Tetrapod Limbs	500



Loss of Limbs in Amphibians and Reptiles	500
Loss of Limbs in Snakes	500
Loss of Forelimbs in Pythons	501
<b>Loss/Reduction of Limbs in Aquatic Mammals</b>	503
Neo-Darwinian Explanation	506
Epigenetic Explanation	506
<b>Loss of Lungs in Salamanders</b>	507
Loss of Eyes in the Mole Rat <i>Spalax ehrenbergi</i>	508
<b>Loss of Characters in Cave-Dwelling Animals</b>	509
<b>Loss of Eyes in <i>Astyanax faciatus (mexicanus)</i>: Epigenetics of an Evolutionary Event</b>	510
Neo-Darwinian Explanation	513
Epigenetic Explanation	514
<b>Loss of Pigmentation in the Cavefish <i>A. mexicanus</i></b>	519
Neo-Darwinian Explanation	520
Epigenetic Explanation	520
<b>Loss the Male Conspicuous Coloration in Lizards</b>	521
<b>Loss of Sexual Dichromatism in Birds</b>	521
<b>Loss of Adult Stage of Development—Pedomorphosis in Insects</b>	522
<b>Loss of Terrestrial Mature Stage in Amphibians—Pedomorphosis</b>	522
Neo-Darwinian Explanation	525
Epigenetic Explanation	525
<b>Loss of Behaviors</b>	526
Loss of the Acoustic Startle Response in Moths Endemic to Bat-Free Habitats	526
<b>References</b>	528
<b>Further Reading</b>	533

## 12. Evolution by Reverting to Ancestral Characters 535

<b>Evolutionary Reversions: The Course of Evolution Is Not Unidirectional</b>	535
<b>Atavisms: Ancestral Developmental Pathways May Be Conserved and Reactivated</b>	539
Neo-Darwinian Explanation	541
Epigenetic Explanation	541
<b>Evolutionary Reversions in Nature</b>	541
Reversion of Shell Coiling in Gastropods	541
Reversion of Cartilaginous Skeleton in Fish	542
Reversion of the Hydrodynamic Body Shape in Marine Mammals	543
Reversion of Wings in Stick Insects	544
Reversion of Eyes in Ostracods	544
Reversion of Limbs in Snakes	545
Reappearance of <i>Musculus IFE</i> in the Bowerbird <i>Loria loriae</i> and the New Zealand Thrush, <i>Turnagra capensis</i>	545
Evolutionary Reversion of Life Histories	545
<b>Evolutionary Reversions in Experiments</b>	546
Experimental Reversion of Teeth in Birds	546
<b>Reversion of Life History Characters</b>	548



Reversion of Ancestral Modes of Development in Gastropods	548
Reversion of Direct and Biphase Development in Plethodontid Salamanders	548
Reversion of Ancestral Reproductive Modes in Vertebrates	550
Reversion to Ancestral Oviparity in Sharks and Rays	551
Reversion of Viviparity in Reptiles	551
Reevolution of Oviparity in Bovides	552
Experimental Reversion of Ancestral Characters	553
Experimental Reversion of Ancestral Characters in <i>Drosophila</i>	553
Experimental Reversion of "Hip Glands" in Voles	555
Reversion of Sexuality in Parthenogenetic Lizards	556
Modified Ancestral Structures Reappear Stepwise	557
References	558
Further Reading	561

<b>13. Epigenetics of Sympatric Speciation—Speciation as a Mechanism of Evolution</b>	<b>563</b>
Recognition of the Reality of Sympatric Speciation	563
Sympatric Speciation: No Changes in Genes Are Involved	564
Natural Selection and Sexual Selection in Sympatric Speciation	567
Neurocognitive Populational Breakup	570
Reproductive Isolation via Mate Choice	570
Evolution of Mating Preferences	572
Fisher's Runaway Hypothesis	572
The "Good Gene" Hypothesis	572
Sensory Exploitation Hypothesis	574
Neural-Cognitive Mechanisms of Sympatric Reproductive Isolation	575
Evolution of Receiver Biases	576
Evolution of Sender's Signaling	581
Mate Recognition System	583
Neurocognitive Mechanisms of Reproductive Isolation	589
Visual-cognitive Mechanism of Reproductive Isolation	589
Neural Reception and Processing of Bioluminescent Signals	591
Olfactory-Cognitive Mechanism of Reproductive Isolation	593
Neural Reception and Processing of Olfactory Signals	593
Olfactorily Determined Reproductive Isolation in Sympatry	596
Auditory-Cognitive Reproductive Isolation	598
Neural Reception and Processing of Acoustic Signals	598
The Song Circuit in the Brain of Birds	600
Acoustically Determined Reproductive Isolation in Sympatry	601
Electrocognitive Mechanism of Reproductive Isolation	605
Electrogenesis in Fish	605
The Structure of the System of Electoreception in Fish	606
Electrosensory Communication in Social and Reproductive Behavior	610
Evolution of Electrosignals, Electrocognitive Isolation of Populations, and Sympatric Speciation in Fish	614



Neo-Darwinian Explanation of Sympatric Reproductive Isolation and Speciation of <i>Brienomyrus</i> spp.	616
Epigenetic Explanation of Sympatric Reproductive Isolation and Speciation of <i>Brienomyrus</i> spp.	616
Brain, Behavior, and Evolution	617
Behavioral Drive or Brain Size-Environmental Change Hypothesis	618
Neo-Darwinian Explanation of the Correlation Between the Brain Size and Evolutionary Rates	620
Epigenetic Explanation of the Correlation Between the Brain Size and Evolutionary Rates	621
Neurocognitive Sympatric Speciation	621
Neurocognitive Basis of Sympatric Speciation	622
Neurocognitive Sympatric Speciation in Nature	624
Neurocognitive Sympatric Speciation in Insects	624
Sexual Neurocognitive Sympatric Speciation	624
Nonsexual Neurocognitive (Host Plant Shifting) Sympatric Speciation	625
Neo-Darwinian Explanation of Sympatric Speciation by Host Plant Shifting	628
Epigenetic Explanation of Sympatric Speciation by Host Plant Shifting	630
Neurocognitive Sympatric Speciation in Fish	631
Neurocognitive Sympatric Speciation in Salamanders	634
Despeciation or Fusion of Species	634
References	635
Further Reading	645
<b>4. Epigenetics in Health and Disease</b>	647
Health, Inflammation, and Disease	647
Homeostasis and Stress	648
Evolution of Stress Response	655
Immunity	656
Innate Immunity—The Front Line of Host Defense Against Infection	658
Acquired/Humoral Immunity—The Second Line of Defense	664
Humoral Immunity	670
Immune Tolerance and the Development of Tolerance to Self-Antigens	688
Neural Control of Allergy	691
Autoimmunity and Autoimmune Diseases	694
Epigenetics of Carcinogenesis	698
Etiology of Cancer	699
Cancer and DNA Methylation	702
Cancer and Histone Modifications	703
The Neurogenic Etiology of Cancer	707
References	716
Further Reading	730



<b>15. Plant Epigenetics</b>	733
<b>Aspects of Plant Epigenetics</b>	733
Embryonic Development in Plants	733
Formation of Gametophytes	733
Endosperm Development	736
Seed Development in <i>Arabidopsis thaliana</i>	736
Seed Maturation and Dormancy	739
Germination	741
<b>Epigenetic Modifications in Plant Development</b>	744
DNA Methylation	744
Histone and Chromatin Modifications	745
Stem Cell Niches in Plants	746
<b>Transcriptional Regulation</b>	747
Transcription of miRNA Genes	747
Developmental Switches in Plants	748
<b>Plant Growth and Development</b>	751
The Vegetative Phase	751
The Reproductive Stage	752
Vernalization	754
On the Control System in Plants	756
<b>Plant Hormones</b>	758
Auxin	759
Cytokinins	761
Abscisic Acid	763
Brassinoids	764
Gibberellins	766
<b>Epigenetics of Plant Development</b>	767
miRNA in Regulation of Gene Expression	767
Transgenerational Inheritance in Plants	769
<b>References</b>	774
<b>Further Reading</b>	781
<b>Index</b>	783