



CRC Press
Taylor & Francis Group



Fourth Edition

Insect Physiology and Biochemistry

James L. Nation, Sr.

Insect Physiology and Biochemistry

Fourth Edition

b14620665
g 185530 (3
i 22607274



James L. Nation, Sr.



CRC Press

Taylor & Francis Group

Boca Raton London New York

300-14-2
CRC Press is an imprint of the
Taylor & Francis Group, an informa business

Contents

Preface.....	xix
Author Biography.....	xxi
Chapter 1 Embryogenesis	1
1.1 Introduction	1
1.2 Morphogenesis.....	1
1.2.1 Egg, Fertilization, and Zygote Formation	1
1.2.2 Variations in Zygotic Nucleus Cleavage, Formation of Energids, and Blastoderm Formation.....	3
1.2.2.1 Aptyygota	4
1.2.2.2 Hemimetabola.....	5
1.2.2.3 Holometabola.....	6
1.2.3 Formation of the Germ Band	6
1.2.4 Gastrulation	7
1.2.5 Germ Band Elongation.....	8
1.2.6 Blastokinesis and Extraembryonic Membranes.....	8
1.3 Genetic Control of Embryogenesis.....	11
1.3.1 Development of a Model for Patterning	12
1.3.1.1 The <i>bicoid</i> Gene and Anterior Determination in <i>Drosophila</i>	12
1.3.1.2 Posterior Group Genes and Posterior Pattern Formation	13
1.3.1.3 Genes Required in the Acron and Telson	14
1.3.1.4 Dorsal–Ventral Axis	14
1.4 Segmentation Genes	14
1.5 Homeotic Genes	15
1.5.1 Homeobox	16
1.6 Organogenesis	16
1.6.1 Neurogenesis	16
1.6.2 Development of the Gut.....	17
1.6.3 Malpighian Tubules.....	17
1.6.4 Tracheal System	17
1.6.5 Oenocytes	17
1.6.6 Wing Development.....	17
1.6.7 Cuticle Secretion in the Embryo	18
1.6.8 Cell Movements During Embryogenesis.....	18
1.6.9 Programmed Cell Death: Apoptosis	18
1.7 Hatching	18
1.8 Imaginal Discs.....	18
1.9 Summary and Conclusions	20
1.10 Review and Self-Study Questions	21
References Added to 4th Edition.....	21
Foundation References	23
Chapter 2 Digestion.....	27
2.1 Introduction	27
2.2 Relationships between Food Habits and Gut Structure and Function.....	27
2.2.1 Plant vs. Animal Origin: Solid vs. Liquid Diet.....	27
2.3 Major Structural Regions of the Gut	28
2.3.1 Foregut.....	28
2.3.2 Midgut.....	30
2.3.3 Hindgut.....	30

2.4	Midgut Cell Types	31
2.4.1	Columnar Cells.....	31
2.4.2	Regenerative Cells.....	31
2.4.3	Goblet Cells.....	32
2.5	Microvilli or Brush Border of Midgut Cells	33
2.6	Glycocalyx	34
2.7	Peritrophic Matrix	34
2.7.1	Functions of the Peritrophic Matrix	35
2.8	Digestive Enzymes	36
2.8.1	Carbohydrate-Digesting Enzymes	37
2.8.2	Lipid Digesting Enzymes	37
2.8.3	Protein-Digesting Enzymes.....	37
2.8.4	Do Proteinase Inhibitors in the Food Influence Evolution of Proteinase Secreted?	38
2.9	Hormonal Influence on Midgut	39
2.10	Countercurrent Circulation of Midgut Contents and Absorption of Digested Products.....	40
2.11	Transepithelial and Oxidation–Reduction Potential of the Gut	41
2.12	Gut pH	42
2.13	Hematophagy: Feeding on Vertebrate Blood	44
2.14	Digestive System Morphology and Physiology in Major Insect Orders	44
2.14.1	Orthoptera	44
2.14.2	Dictyoptera	44
2.14.3	Isoptera	45
2.14.4	Hemiptera	45
2.14.5	Homoptera.....	46
2.14.6	Coleoptera	46
2.14.7	Hymenoptera	46
2.14.8	Diptera.....	47
2.14.9	Lepidoptera.....	47
2.15	Insect Gut as a Potential Target for Population Management and Control of the Spread of Plant and Animal Disease Organisms.....	48
2.16	Summary/Conclusions.....	48
2.17	Review and Self-Study Questions	49
	References Added to 4th Edition.....	49
	Foundation References	51
Chapter 3	Nutrition	57
3.1	Introduction	57
3.2	Importance of Balance and Self-Selection of Nutritional Components	58
3.3	Ability of Insects to Self-Select Nutritional Components	59
3.4	Requirements for Specific Nutrients	60
3.4.1	Nitrogen Source: Proteins and Amino Acids	60
3.4.2	Amino Acids	61
3.4.3	Carbohydrates.....	62
3.4.4	Lipids.....	63
3.4.5	Sterols	63
3.4.6	Polyunsaturated Fatty Acids	64
3.4.7	Vitamins	64
3.4.8	Minerals	65
3.5	Techniques and Dietary Terms Used in Insect Nutrition Studies	67
3.6	Criteria for Evaluating Nutritional Quality of a Diet	67
3.7	Measures of Food Intake and Utilization	67
3.8	Phagostimulants.....	68
3.9	Feeding Deterrents	69
3.10	Summary and Conclusions	70
3.11	Review and Self-Study Questions	70
	References Added to 4th Edition.....	71
	Foundation References	72

2.4	Midgut Cell Types	31
2.4.1	Columnar Cells.....	31
2.4.2	Regenerative Cells.....	31
2.4.3	Goblet Cells.....	32
2.5	Microvilli or Brush Border of Midgut Cells	33
2.6	Glycocalyx.....	34
2.7	Peritrophic Matrix	34
2.7.1	Functions of the Peritrophic Matrix.....	35
2.8	Digestive Enzymes	36
2.8.1	Carbohydrate-Digesting Enzymes	37
2.8.2	Lipid Digesting Enzymes	37
2.8.3	Protein-Digesting Enzymes.....	37
2.8.4	Do Proteinase Inhibitors in the Food Influence Evolution of Proteinase Secreted?	38
2.9	Hormonal Influence on Midgut	39
2.10	Countercurrent Circulation of Midgut Contents and Absorption of Digested Products.....	40
2.11	Transepithelial and Oxidation–Reduction Potential of the Gut	41
2.12	Gut pH	42
2.13	Hematophagy: Feeding on Vertebrate Blood	44
2.14	Digestive System Morphology and Physiology in Major Insect Orders	44
2.14.1	Orthoptera	44
2.14.2	Dictyoptera	44
2.14.3	Isoptera	45
2.14.4	Hemiptera	45
2.14.5	Homoptera	46
2.14.6	Coleoptera	46
2.14.7	Hymenoptera	46
2.14.8	Diptera.....	47
2.14.9	Lepidoptera.....	47
2.15	Insect Gut as a Potential Target for Population Management and Control of the Spread of Plant and Animal Disease Organisms.....	48
2.16	Summary/Conclusions.....	48
2.17	Review and Self-Study Questions	49
	References Added to 4th Edition.....	49
	Foundation References	51
Chapter 3	Nutrition	57
3.1	Introduction	57
3.2	Importance of Balance and Self-Selection of Nutritional Components	58
3.3	Ability of Insects to Self-Select Nutritional Components	59
3.4	Requirements for Specific Nutrients	60
3.4.1	Nitrogen Source: Proteins and Amino Acids	60
3.4.2	Amino Acids	61
3.4.3	Carbohydrates.....	62
3.4.4	Lipids.....	63
3.4.5	Sterols	63
3.4.6	Polyunsaturated Fatty Acids	64
3.4.7	Vitamins	64
3.4.8	Minerals	65
3.5	Techniques and Dietary Terms Used in Insect Nutrition Studies	67
3.6	Criteria for Evaluating Nutritional Quality of a Diet	67
3.7	Measures of Food Intake and Utilization	67
3.8	Phagostimulants.....	68
3.9	Feeding Deterrents	69
3.10	Summary and Conclusions	70
3.11	Review and Self-Study Questions	70
	References Added to 4th Edition.....	71
	Foundation References	72

Chapter 4	Integument and Molting	77
4.1	Introduction	77
4.2	Structure of the Integument.....	77
4.2.1	Cuticulin Envelope	78
4.2.2	Epicuticle.....	78
4.2.3	Procuticle.....	78
4.2.4	Pore Canals and Wax Channels	79
4.2.5	Epidermal Cells.....	79
4.3	Molting and Formation of New Cuticle.....	82
4.3.1	Apolysial Space.....	83
4.3.2	Molting Fluid Secretion.....	83
4.3.3	New Cuticle Formation	83
4.3.4	Reabsorption of Molting Fluid.....	84
4.4	Ecdysis.....	84
4.4.1	Shedding the Old Cuticle: Ecdysis of the Adult.....	86
4.4.2	Post-Ecdysis Wing Expansion and Water Proofing the New Cuticle.....	87
4.4.3	Sclerotization of Cuticle	87
4.5	Chemical Composition of Cuticle	90
4.5.1	Chitin.....	91
4.5.2	Biosynthesis of Chitin	93
4.5.3	Cuticular Proteins.....	95
4.5.4	Resilin.....	96
4.5.5	Stage-Specific Differences in Cuticle Proteins	97
4.5.6	Protective Functions of Cuticle Proteins	97
4.5.7	Cuticular Lipids.....	98
4.6	Mineralization of Insect Cuticles	99
4.7	Capture of Atmospheric Water on Cuticular Surfaces	100
4.8	Summary and Conclusions	100
4.9	Review and Self-Study Questions	101
	References Added to 4th Edition	101
	Foundation References	102
Chapter 5	Hormones and Development	107
5.1	Introduction	107
5.2	Interplay of PTTH, Ecdysteroids, and Juvenile Hormone Controls Development	107
5.3	Brain Neurosecretory Cells and Prothoracitropic Hormone (PTTH)	111
5.3.1	Source and Chemistry	111
5.3.2	Bioassay for PTTH Activity	111
5.3.3	Stimuli for Secretion of PTTH.....	112
5.3.4	Secretion of PTTH after Brain Activation by Stretch Receptors.....	113
5.3.5	Gated PTTH Secretion in Tobacco Hornworm.....	113
5.3.6	Secretion of PTTH after Brain Activation by Cold Exposure	113
5.3.7	Regulation of Tissue and Hemolymph Levels of PTTH	114
5.3.8	Mode of Action of PTTH	114
5.4	Prothoracic Glands and Ecdysteroids.....	114
5.4.1	Biosynthesis of Ecdysone	116
5.4.2	Conversion of Ecdysone into 20-Hydroxyecdysone.....	117
5.4.3	Molecular Diversity in the Structure of the Molting Hormone.....	118
5.4.4	Assays for Ecdysteroids.....	118
5.4.5	Radioimmunoassay for Ecdysone and Related Ecdysteroids.....	119
5.4.6	Assay by Physicochemical Techniques	119
5.4.7	Tissues and Cell Cultures Used in Assays	120
5.4.8	Degradation of Ecdysone	121
5.4.9	Virus Degradation of Host Ecdysteroids.....	121
5.4.10	Dependence of Some Parasitoids on Host Ecdysteroids	121
5.5	Corpora Allata and Juvenile Hormones	121

5.5.1	Glandular Source and Chemistry of Juvenile Hormones.....	121
5.5.2	Assays for JH Activity.....	123
5.5.3	Regulation of the Tissue and Hemolymph Levels of JH.....	123
5.5.4	Growth Regulators and Compounds Cytotoxic to the Corpora Allata.....	125
5.5.5	Cellular Mode of Action and Receptors for JH.....	127
5.5.6	Downstream Transcription Factors	129
5.6	Mode of Action of Ecdysteroids at the Gene Level.....	129
5.6.1	Chromosomal Puffs.....	129
5.6.2	Identification and Isolation of an Ecdysteroid Receptor	131
5.6.3	Differential Tissue and Cell Response to Ecdysteroids	132
5.7	Possible Timer Gene in the Molting Process.....	133
5.8	Ecdysone–Gene Interaction Ideas Stimulated Vertebrate Work.....	134
5.9	Development of Eyespots in Wings of Lepidoptera	134
5.10	Summary and Conclusions	134
5.11	Review and Self-Study Questions	135
	References Added to 4th Edition.....	136
	Foundation References	138
Chapter 6	Biological Rhythms.....	143
6.1	Introduction	143
6.2	Characteristics of Circadian and Photoperiodic Rhythms	143
6.3	Molecular Basis for the Circadian Clock	144
6.4	Evidence for Clock Genes in Many Insects.....	146
6.4.1	Circadian Regulation of Hormone Secretion	148
6.4.2	Circadian Clock Influence in Peripheral Organs and Tissues.....	149
6.4.3	Circadian Clock Influence in Social Behavior of Honeybees	150
6.4.4	Circadian Clock Influence in Reproduction.....	150
6.5	Photoperiodic Response: One Clock, Two Clocks, or Multiple Clocks?.....	153
6.6	Clock Models Based on Experimental Responses of Insects to Varying Light/Dark Regimes	154
6.6.1	Hourglass Model	155
6.6.2	External Coincidence Model	155
6.6.3	Internal Coincidence Model	156
6.6.4	Resonance Model	156
6.6.5	Summary Results from Model Experiments.....	156
6.7	Summary and Conclusions	156
6.8	Review and Self-Study Questions	157
	References Added to 4th Edition.....	157
	Foundation References	159
Chapter 7	Diapause	165
7.1	Introduction	165
7.2	Diapause: A Survival Strategy	165
7.3	Phases of Diapause	167
7.3.1	Prediapause: Induction and Preparation.....	168
7.3.2	Diapause: Initiation and Maintenance.....	169
7.3.3	Diapause Termination	169
7.4	Hormonal Control of Diapause	169
7.4.1	Embryonic Diapause	169
7.4.2	Larval Diapause	170
7.4.3	Pupal Diapause.....	170
7.4.4	Adult Diapause/Reproductive Diapause	171
7.5	Role of Daily and Seasonal Biological Clocks in Diapause.....	172
7.6	Diapause and Gene Expression	172
7.7	Nutrient Accumulation for Diapause and the Storage and Conservation of Nutrients During Diapause.....	172

7.8	Molecular Studies of Diapause.....	173
7.9	A Pre-Diapause Strategy – Cold Tolerance.....	174
7.10	Summary and Conclusions.....	175
7.11	Review and Self-Study Questions	175
	References Added to 4th Edition.....	175
	Foundation References	177
Chapter 8	Intermediary Metabolism.....	181
8.1	Introduction	181
8.2	Energy Demands for Insect Flight	182
8.3	Metabolic Stores	183
8.3.1	Carbohydrate Resources	183
8.3.1.1	Trehalose Resources	183
8.3.1.2	Glycogen: Storage and Synthesis.....	185
8.4	Hormones Controlling Carbohydrate Metabolism.....	186
8.5	Pathways of Metabolism Supporting Intense Muscular Activity, Such as Flight	186
8.5.1	Glycolysis	186
8.5.1.1	The Glycerol-3-Phosphate Shuttle and Regeneration of NAD ⁺	188
8.5.1.2	Significance and Control of the Glycerol-3-Phosphate Shuttle	190
8.5.2	The Krebs Cycle.....	190
8.5.2.1	Control of Krebs Cycle Metabolism and Regulation of Carbohydrate Metabolism in Flight Muscles	192
8.5.3	The Electron Transport System.....	192
8.5.4	Proline as a Fuel for Flight	194
8.5.5	Mobilization and Use of Lipids for Flight Energy	197
8.5.5.1	Transport of Lipids by Lipophorin	200
8.5.5.2	Activation of Fatty Acids, Entry into Mitochondria, and β-Oxidation	201
8.6	Summary and Conclusions	202
8.7	Review and Self-Study Questions	203
	References Added to 4th Edition.....	203
	Foundation References	204
Chapter 9	The Nervous System: Anatomy and Physiology	207
9.1	Introduction	207
9.2	Central Nervous System (CNS)	208
9.3	The Brain.....	208
9.3.1	Protocerebrum.....	209
9.3.2	Deutocerebrum.....	211
9.3.3	Tritocerebrum.....	211
9.4	Ventral Ganglia.....	212
9.5	Oxygen and Glucose Supply to the Brain and Ganglia	213
9.6	The Neuropil.....	213
9.7	Hemolymph–Brain (CNS) Barrier	213
9.8	Neurons: Building Blocks of a Nervous System	214
9.8.1	Afferent or Sensory Neurons	214
9.8.2	Efferent or Motor Neurons	214
9.8.3	Interneurons	215
9.8.4	Glial Cells.....	215
9.9	Nerve Cell Responses to Stimuli.....	216
9.9.1	Graded Responses	216
9.9.2	Spike Potentials	216
9.10	The Physiological Basis for Neuronal Responses to Stimuli	216
9.10.1	Membrane Ion Channels: Bioelectric Potentials	216
9.10.2	The Resting Potential	219
9.10.3	The Action Potential: Sodium Activation	220

9.10.4	Sodium Inactivation and Repolarization	221
9.10.5	Measurement of Ion Fluxes: Voltage Clamp Technique	222
9.10.6	Conduction of the Action Potential: Local-Circuit Theory	222
9.11	The Synapse: Excitatory and Inhibitory Postsynaptic Potentials	223
9.11.1	Acetylcholine-Mediated Synapses	224
9.11.2	Nicotinic and Muscarinic Receptors in Insects	225
9.11.3	Electric Transmission across Synapses	225
9.11.4	Neuromuscular Junctions	226
9.12	Summary and Conclusions	226
9.13	Review and Self-Study Questions	227
	References Added to 4th Edition	227
	Foundation References	228
Chapter 10	The Nervous System: Selected Roles in Behavior	231
10.1	Introduction	231
10.2	Neuropeptides	231
10.3	Selected Behaviors	232
10.3.1	Sleep in Insects	232
10.3.2	Learning in Insects	234
10.3.3	Gustation and Feeding in Insects	235
10.4	Motor Programs	237
10.4.1	A Motor Program that Controls Walking	237
10.4.2	A Motor Pattern for Rhythmic Breathing	238
10.4.3	Escape Behavior and Trapping of Prey: Role of Giant Axons	238
10.5	Summary and Conclusions	240
	Acknowledgments	241
10.6	Self-Study Questions	241
	References Added to 4th Edition	241
	Foundation References	245
Chapter 11	Muscles Physiology and Kinematics	247
11.1	Introduction	247
11.2	Basic Muscle Structure and Function	247
11.2.1	Macro- and Microstructure of Muscle	248
11.2.2	Muscle Attachments to the Exoskeleton	249
11.2.3	Skeletal Muscle	250
11.2.4	Polyneuronal Innervation and Multiterminal Nerve Contacts	250
11.2.5	The Transmitter Chemical at Nerve–Muscle Junctions	252
11.3	Synchronous and Asynchronous Muscles	252
11.4	Muscle Proteins and Physiology of Contraction	254
11.4.1	The Active State: Binding of Myosin Heads to Actin and the Sliding of Filaments	254
11.4.2	Release of Myosin Heads from Actin	255
11.5	Muscles Involved in General Locomotion, Running, and Jumping	256
11.5.1	Adaptations for Running, Walking, and Survival	256
11.5.2	Adaptations for Jumping	257
11.6	Sound Production: Tymbal and Stridulatory Muscle	258
11.6.1	Tymbal Morphology and Physiology	258
11.6.2	Stridulatory Muscle Physiology	259
11.7	Insect Chill Response: Neuromuscular Physiology	260
11.8	Morphology and Physiology of Nonskeletal Muscle	260
11.8.1	Visceral Muscles	260
11.8.2	Heart Muscle	261
11.8.3	Alary Muscles	261
11.9	Summary and Conclusions	261
11.10	Review and Self-Study Questions	262

References Added to 4th Edition.....	262
Foundation References	263
Chapter 12 Insect Flight.....	267
12.1 Introduction	267
12.2 Thoracic Structure, Wing Hinges, and Muscle Groups Involved in Flight.....	268
12.3 Wing Strokes	269
12.4 Multiple Contractions from Each Volley of Nerve Impulses to Asynchronous Muscles.....	270
12.5 Flight in Dragonflies and Damselflies.....	270
12.6 Aerodynamics of Lift and Drag Forces Produced by Wings	272
12.6.1 Lift Forces Generated by Clap and Fling Wing Movements	272
12.6.2 Lift Forces Derived from Drag and Delayed Stall.....	273
12.7 Hovering Flight.....	274
12.8 Control of Pitch and Twisting of Wings	275
12.9 Power Output of Flight Muscles.....	275
12.10 Metabolic Activity of Wing Muscles.....	276
12.11 Flight Behavior	277
12.12 Summary and Conclusions	277
12.13 Review and Self-Study Questions	278
References Added to 4th Edition	278
Foundation References	279
Chapter 13 Sensory Systems.....	283
13.1 Introduction	283
13.2 External and Internal Receptors Monitor the Environment.....	284
13.3 General Functional Classification of Sensory Receptors	284
13.3.1 Receptors with Multiple Pores	285
13.3.2 Receptors with a Single Pore.....	285
13.3.3 Receptors without Pores	285
13.4 Mechanoreceptors	286
13.4.1 Structure of a Simple Tactile Hair: A Mechanoreceptor Sensillum	286
13.4.2 Hair Plates	286
13.4.3 Chordotonal Sensilla	286
13.4.4 Subgenual Organs.....	287
13.4.5 Tympanal Organs: Specialized Organs for Airborne Sounds.....	288
13.4.6 Johnston's Organ	290
13.4.7 Simple Chordotonal Organs	291
13.4.8 Thermoreceptors and Hygroreceptors.....	291
13.4.9 Infrared Reception	292
13.5 Chemoreceptors.....	293
13.5.1 Olfactory Sensilla: Dendritic Fine Structure	293
13.5.2 Contact Chemoreceptors—Gustatory Receptors	294
13.5.3 Specialists vs. Generalists among Chemoreceptors	295
13.5.4 Stimulus-Receptor Excitation Coupling	296
13.6 Summary and Conclusions	296
13.7 Review and Self-Study Questions	297
References Added to 4th Edition	297
Foundation References	298
Chapter 14 Vision	301
14.1 Introduction	301
14.2 Compound Eye Structure	302
14.3 Dioptric Structures	303
14.4 Corneal Layering.....	305

14.5 Retinula Cells	305
14.6 Rhabdomeres	305
14.7 Electrical Activity of Retinula Cells	305
14.8 Neural Connections in the Optic Lobe.....	306
14.9 Ocelli	306
14.10 Larval Eyes: Stemmata.....	307
14.11 Dermal Light Sense.....	307
14.12 Chemistry of Insect Vision.....	309
14.13 Visual Cascade	309
14.14 Regulation of the Visual Cascade	309
14.15 Color Vision.....	310
14.16 Vision is Important in Behavior	312
14.17 Nutritional Need for Carotenoids in Insects.....	312
14.18 Detection of Plane-Polarized Light	313
14.19 Visual Acuity	314
14.20 Summary and Conclusions	316
14.21 Review and Self-Study Questions	316
References Added to 4th Edition.....	316
Foundation References	317
Chapter 15 Circulatory System.....	321
15.1 Introduction: Circulatory System	321
15.2 Dorsal Vessel: Heart and Aorta.....	321
15.2.1 Alary Muscles	324
15.2.2 Ostia	324
15.2.3 Heartbeat	325
15.2.4 Ionic Influences on Heartbeat	326
15.2.5 Nerve Supply to the Heart.....	326
15.2.6 Cardioactive Secretions.....	326
15.3 Accessory Pulsatile Hearts.....	327
15.4 Hemocytes	328
15.4.1 Functions of Hemocytes	330
15.4.2 Hemocytopoietic Tissues and Origin of Hemocytes	330
15.4.3 Number of Circulating Hemocytes	332
15.5 Hemolymph	333
15.5.1 Functions of Hemolymph and Circulation	333
15.5.2 Hemolymph Volume.....	335
15.5.3 Coagulation of Hemolymph	335
15.5.4 Hemolymph pH and Hemolymph Buffers.....	336
15.5.5 Chemical Composition of Hemolymph.....	337
15.5.5.1 Inorganic Ions	337
15.5.5.2 Free Amino Acids.....	338
15.5.5.3 Proteins	338
15.5.5.4 Other Organic Constituents	338
15.6 Rate of Circulation	338
15.7 Hemoglobin	339
15.8 Summary and Conclusions	339
15.9 Review and Self-Study Questions	340
References Added to 4th Edition.....	340
Foundation References	342
Chapter 16 Immunity	345
16.1 Introduction	345
16.2 Physical Barriers to Invasion	345
16.3 Recognition of Nonself.....	346
16.4 Cellular Immune Reactions	347

16.5	Synthesis of Antifungal and Antibacterial Peptides	349
16.6	Toll, IMD, JNK, and JAK-STAT Are Pathways for Defense Responses	350
16.6.1	Toll Pathway	351
16.6.2	IMD Pathway	352
16.6.3	JNK Pathway	352
16.6.4	JAK-STAT Pathway	352
16.7	C-Type Lectins	352
16.8	Serpins	352
16.9	Ecology, Behavior, and Immunity	353
16.9.1	Effects of Climate Change on Insect Immune Responses	353
16.9.2	Limitation of Nutritional Resources May Alter Immune Response	354
16.10	Cost of Defense: To Defend or Not? What Are the Trade-Offs?.....	354
16.11	Coevolutionary Race between Parasitoid Escape Mechanisms and Host Defense Mechanisms	355
16.12	Autoimmune Consequences of Some Defense Reactions	356
16.13	Gender Differences in Immune Responses	356
16.14	Summary and Conclusions	356
16.15	Review and Self-Study Questions	357
	References Added to 4th Edition.....	357
	Foundation References	360
Chapter 17	Respiration	365
17.1	Introduction	365
17.2	Structure of the Tracheal System	366
17.2.1	Tracheae and Tracheole Structure.....	366
17.2.2	Plasticity in the Tracheal System	367
17.2.3	Spiracle Structure and Function	367
17.2.4	Tracheal Epithelium	369
17.2.5	Development of New Tracheoles.....	369
17.2.6	Air Sacs	370
17.2.7	Molting of Tracheae	370
17.3	Tracheal Supply to Tissues and Organs.....	371
17.3.1	Adaptations of Tracheae to Supply Flight Muscles.....	371
17.4	Ventilation and Diffusion of Gases within the System	373
17.4.1	Simple Diffusion is Usually Not Adequate.....	373
17.4.2	Active Ventilation of Tracheae	373
17.4.3	Diffusion from Tracheoles to Mitochondria	376
17.5	Discontinuous Gas Exchange	376
17.6	Water Balance during Flight	378
17.7	Gas Exchange in Aquatic Insects	379
17.7.1	Compressible Gas Gills	379
17.7.2	Incompressible Gas Gills: A Plastron	380
17.7.3	Use of Aquatic Plants as Air Source	380
17.7.4	Cutaneous Respiration: Closed Tracheal System in Some Aquatic Insects	381
17.8	Respiration in Endoparasitic Insects	383
17.9	Respiratory Pigments	383
17.10	Respiration in Eggs and Developing Embryos	383
17.11	Nonrespiratory Functions of the Tracheal System	384
17.12	Summary and Conclusions	384
17.13	Review and Self-Study Questions	385
	References Added to 4th Edition.....	385
	Foundation References	386
Chapter 18	Excretion	391
18.1	Introduction	391
18.2	Malpighian Tubules	391

18.3	Malpighian Tubule Cells	393
18.4	Formation of Primary Urine in Malpighian Tubules	394
18.5	Proton Pump as Driving Mechanism for Urine Formation and Homeostasis	394
18.6	Possibilities for Selectively Disrupting Water and Ion Homeostasis for Insect Control	396
18.7	Selective Reabsorption in the Hindgut	397
18.7.1	Anatomical Specialization of Hindgut Epithelial Cells	397
18.7.2	Secretion and Reabsorption in the Ileum	399
18.7.3	Reabsorption in the Rectum	399
18.8	Role of the Excretory System in Maintaining Homeostasis	399
18.8.1	Electrolyte Homeostasis	400
18.8.2	Water Homeostasis	401
18.8.2.1	Diuretic Hormones	401
18.8.2.2	Antidiuretic Hormones	403
18.8.3	Acid–Base Homeostasis	403
18.8.4	Nitrogen Homeostasis	403
18.8.4.1	Ammonia Excretion	403
18.8.4.2	Uric Acid Synthesis and Excretion	405
18.9	Cryptonephridial Systems	407
18.10	Summary and Conclusions	408
18.11	Review and Self-Study Questions	408
	References Added to 4th Edition	409
	Foundation References	410
Chapter 19	Semiochemicals.....	415
19.1	Introduction	415
19.2	Classes of Semiochemicals	415
19.3	Importance of the Olfactory Sense in Insects	416
19.4	Active Space Concept	418
19.5	Pheromones Classified According to Behavior Elicited	418
19.6	Pheromone Parsimony	418
19.7	Chemical Characteristics of Semiochemicals	419
19.8	Insect Receptors and Odorant-Binding Proteins	421
19.8.1	Pheromone-Binding Proteins	421
19.8.2	Signal Transduction and Receptor Response	423
19.8.3	Pheromone Inactivation and Clearing of the Receptor	424
19.8.4	Do Insects Smell the Blend or Just the Major Components?	425
19.9	Information Coding and Processing	426
19.9.1	Structure of Odor Plumes	426
19.9.2	Pheromone Signal Processing	428
19.10	Hormonal Control of Pheromone Synthesis and Release	429
19.11	Biosynthesis of Pheromones	430
19.12	Geographical and Population Differences and Evolution of Pheromone Blends	433
19.13	Practical Applications of Pheromones	434
19.14	Summary and Conclusions	436
19.15	Review and Self-Study Questions	436
	References Added to 4th Edition	437
	Foundation References	439
Chapter 20	Reproduction	447
20.1	Introduction	447
20.2	Female Reproductive System	447
20.2.1	Structure of Ovaries	447
20.2.1.1	Panoistic Ovarioles	449
20.2.1.2	Telotrophic Ovarioles	449
20.2.1.3	Polytrophic Ovarioles	449

20.2.1.4	Oviposition.....	450
20.2.2	Nutrients for Oogenesis.....	450
20.2.3	Hormonal Regulation of Ovary Development and Synthesis of Egg Proteins	451
20.3	Vitellogenins and Yolk Proteins	456
20.3.1	Biochemical Characteristics of Vitellogenins and Yolk Proteins	456
20.3.2	Yolk Proteins of Higher Diptera.....	457
20.4	Sequestering of Vitellogenins and Yolk Proteins by Oocytes.....	457
20.4.1	Patency of Follicular Cells	457
20.4.2	Egg Proteins Produced by Follicular Cells	458
20.4.3	Proteins in Addition to Vitellogenin and Yolk Proteins in the Egg	459
20.5	Formation of the Vitelline Membrane.....	459
20.6	The Chorion.....	460
20.7	Gas Exchange in Eggs	460
20.8	Male Reproductive System.....	460
20.8.1	Apyrene and Eupyrene Sperm of Lepidoptera.....	463
20.8.2	Male Accessory Glands.....	463
20.8.3	Transfer of Sperm.....	464
20.9	Sex Determination.....	464
20.10	Chromosomal Systems for Gender Determination	465
20.11	Summary and Conclusions	466
20.12	Review and Self-Study Questions	466
	References Added to 4th Edition.....	467
	Foundation References	469
Chapter 21	Insect Symbioses	475
21.1	Introduction	475
21.2	Symbioses among Leaf-Cutting Ants, Fungi, and Bacteria.....	476
21.3	Biology of Termites	478
21.3.1	Symbionts in Termites.....	479
21.3.2	Lignocellose Structure	480
21.3.3	Nitrogen Metabolism.....	480
21.3.4	Fungal Culture.....	481
21.4	Bark and Ambrosia Beetles and Their Symbionts	481
21.4.1	Ambrosia Beetles	481
21.4.2	Bark Beetles	483
21.4.3	Fungal Role in Supplementing Limited Nutrients in Wood and Phloem.....	483
21.4.4	Evolution of Fungal Feeding in Bark Beetles	485
21.4.5	Bacteria as Part of the Bark Beetle Holobiont	485
21.4.6	Anthropogenic Effects upon Bark Beetles and Their Symbionts	485
21.5	<i>Buchnera</i> in Aphids.....	486
21.6	Tsetse Fly Symbionts.....	486
21.7	<i>Wolbachia</i>	487
21.7.1	Cytoplasmic Incompatibility Inducing Effect of <i>Wolbachia</i>	488
21.7.2	Parthenogenesis-Inducing Effect of <i>Wolbachia</i>	489
21.7.3	Feminizing Strains of <i>Wolbachia</i>	489
21.8	<i>Burkholderia</i> in Insects	490
21.9	Summary and Conclusions	491
21.10	Self-Study Questions	491
	References Added to 4th Edition.....	492
	Foundation References	494
Chapter 22	Global Climate Change: Present and Future Impact on Insects	503
22.1	Introduction	503
22.2	How Have Insects Responded to Climate: Will Climate Change Bring Greater Damage by Insect Pests?	505

22.3	Acclimation of Insects to Lower Thermal Limits: Their Response to Fluctuating and Extreme Cold.....	506
22.4	Response of Insects to Upper Thermal Limits.....	508
22.5	Will Tropical Insect Be More or Less Impacted by Climate Warming?	509
22.6	Insect Ecophysiology and Climate Change.....	509
22.7	Climate Change is Driving Insect Distributions	510
22.8	Climate Change: Insect Vectors and Infectious Diseases	511
22.9	Summary and Conclusions	513
22.10	Review and Self-Study Questions	513
	Acknowledgments	514
	References	514
Chapter 23	The Genomics Revolution in Entomology	521
23.1	Introduction	521
23.2	Transposable Elements	523
23.2.1	Horizontal and Vertical Transmission of TEs in Insects	523
23.2.2	Additional Ways Transposons Aid Insects.....	523
23.3	Evolutionarily Ancient and Conserved RNAI Pathways in Insects	523
23.3.1	Functions of microRNA	525
23.3.2	The PIWI RNA (piRNA) Pathway: Protection for Germline Cells.....	526
23.3.3	Function of Short Interfering RNA (siRNA) in Insect Antiviral Immunity	526
23.4	Applications of Interfering RNA in Insects	527
23.5	CRISPR/Cas 9 Technology	529
23.5.1	Applications of CRISPR/Cas9 System to Edit Genes in Insects	530
23.5.2	Using CRISPR/Cas9 to Explore Gene Function	532
23.6	Introducing Gene Editing into Educational Programs.....	532
23.7	Summary and Conclusions	532
	Acknowledgments	534
23.8	Review and Self-Study Questions	534
	References	534
Index	539