

# Contents

Classification of the Animal Kingdom (Metazoa) xx  
A Phylogeny of Metazoa xxi  
Geologic Time Scale xxii

## **CHAPTER 1** Introduction 1

Keeping Track of Life 3  
Prokaryotes and Eukaryotes 7  
Where Did Invertebrates Come From? 9  
    The Dawn of Life 10  
    The Ediacaran Period and the Origin of Animals 10  
    The Paleozoic Era (541–251.9 Ma) 11  
    The Mesozoic Era (251.9–66 Ma) 15  
    The Cenozoic Era (66 Ma–present) 16  
Where Do Invertebrates Live? 16  
    Marine Habitats 16  
    Estuaries and Coastal Wetlands 21  
    Freshwater Habitats 21  
    Terrestrial Habitats 22  
    A Special Type of Environment: Symbiosis 22  
Changing Views of Invertebrate Phylogeny 24  
    Legacy Names 25  
    Phylogenetics and Classification Schemes 25  
A Final Introductory Message to the Reader 25

## **CHAPTER 2** Systematics, Phylogeny, and Classifications 27

Phylogeny, Monophyly, Paraphyly, and Polyphyly 28  
Homology 29  
Apomorphy and Plesiomorphy 32  
Challenges of Phylogenetic Inference 32  
Constructing Phylogenies 33  
Biological Classification 35  
Nomenclature 38

## **CHAPTER 3** Introduction to the Animal Kingdom: Animal Architecture and Body Plans 43

Body Symmetry 44  
Cellularity, Body Size, Germ Layers,  
    and Body Cavities 47  
Locomotion and Support 49  
    Reynolds Number 49  
    Ameboid Locomotion 50  
    Cilia and Flagella 50  
    Muscles and Skeletons 52  
Feeding and Digestion 56  
    Intracellular and Extracellular Digestion 56  
    Feeding Strategies 57  
Excretion and Osmoregulation 65  
    Nitrogenous Wastes and Water Conservation 66  
    Osmoregulation and Habitat 66  
    Excretory and Osmoregulatory Structures 67  
Circulation and Gas Exchange 69  
    Internal Transport 69  
    Circulatory Systems 70  
    Hearts and Other Pumping Mechanisms 71  
    Gas Exchange and Transport 71  
Nervous Systems and Sense Organs 75  
    Sense Organs 76  
    Independent Effectors 81  
Bioluminescence 81  
Nervous Systems and Body Plans 81  
Hormones and Pheromones 84  
Reproduction 84  
    Asexual Reproduction 84  
    Sexual Reproduction 86  
    Parthenogenesis 88

<b>CHAPTER 4</b>	<b>Introduction to the Animal Kingdom: Development, Life Histories, and Origin</b>	<b>91</b>
Evolutionary Developmental Biology: Evo-Devo		92
Developmental Tool Kits		92
The Relationship Between Genotype and Phenotype		93
The Evolution of Novel Gene Function		93
Gene Regulatory Networks		93
Eggs and Embryos		95
Eggs		95
Cleavage		95
Orientation of Cleavage Planes		96
Radial and Spiral Cleavage		96
Cell Fates		99
Blastula Types		101
Gastrulation and Germ Layer Formation		101
Mesoderm and Body Cavities		103
Life Cycles: Sequences and Strategies		105
Classification of Life Cycles		105
Indirect Development		107
Settling and Metamorphosis		107
Direct Development		108
Mixed Development		108
Adaptations to Land and Fresh Water		109
Parasite Life Cycles		109
The Relationships Between Ontogeny and Phylogeny		110
The Concept of Recapitulation		110
Heterochrony and Paedomorphosis		111
The Origin of the Metazoa		112
Origin of the Metazoan Condition		112
Historical Perspectives on Metazoan Origins		112
The Origin of Multicellularity		114
The Origin of the Bilateral Condition and the Coelom		115
The Trochaea Theory		116
Closing Thoughts		117
<b>CHAPTER 5</b>	<b>Phylum Porifera: The Sponges</b>	<b>119</b>
Phylum Porifera: The Sponges		120
Taxonomic History and Classification		123
The Poriferan Body Plan		126
Body Structure and the Aquiferous System		127
More on Sponge Cell Types		132
Support		136
Nutrition, Excretion, and Gas Exchange		138
Activity and Sensitivity		143
Reproduction and Development		143
Some Additional Aspects of Sponge Biology		154
Distribution and Ecology		154
Biochemical Agents		154
Growth Rates		155
Symbioses		156
Poriferan Phylogeny		159
The Origin of Sponges		159
Evolution within the Porifera		160
<b>CHAPTER 6</b>	<b>Two Enigmatic Phyla: Placozoa and Ctenophora (The Comb Jellies)</b>	<b>165</b>
Phylum Placozoa		166
Phylum Ctenophora		167
Taxonomic History and Classification		169
The Ctenophoran Body Plan		172
Support and Locomotion		175
Feeding and Digestion		176
Circulation, Excretion, Gas Exchange, and Osmoregulation		179
Nervous System and Sense Organs		179
Reproduction and Development		181
Ctenophoran Phylogeny		183
<b>CHAPTER 7</b>	<b>Phylum Cnidaria: Anemones, Corals, Jellyfish, and Their Kin</b>	<b>185</b>
Taxonomic History and Classification		190
The Cnidarian Body Plan		196
The Body Wall		197
Support		209
Movement		212
Cnidae		215
Feeding and Digestion		218
Defense, Interactions, and Symbiosis		220
Circulation, Gas Exchange, Excretion, and Osmoregulation		227
Nervous System and Sense Organs		227
Reproduction and Development		231
Cnidarian Evolutionary History		240
Earliest Cnidaria		240
Cnidarian Phylogeny		241

## **CHAPTER 8** A Brief Introduction to the Bilateria and Its Major Clades 245

The Bilateria 245

Deuterostomes and Protostomes 246

## **CHAPTER 9** Phylum Xenacoelomorpha: Basal Bilaterians 249

The Basal Bilaterian 249

Phylum Xenacoelomorpha 250

Subphylum Acoelomorpha 252

Class Acoela 252

The Acoel Body Plan 255

Body Wall and External Appearance 255

Body Musculature, Support, and Movement 256

Nutrition, Excretion, and Gas Exchange 257

Nervous Systems and Sense Organs 258

Reproduction and Development 259

Class Nemertodermatida 261

The Nemertodermatid Body Plan 263

Body Structure 263

Cell and Tissue Organization 263

Support and Movement 263

Nutrition, Excretion, Gas Exchange 264

Nervous System 265

Reproduction and Development 265

Subphylum Xenoturbellida 267

The Xenoturbellid Body Plan 268

General Body Structure 268

Support and Movement 269

Nutrition, Excretion, and Gas Exchange 270

Nervous System and Sense Organs 270

Reproduction and Development 270

## **CHAPTER 10** Protostomia, Spiralia, and the Phylum Dicyemida 273

Protostomes and Deuterostomes 273

Spiralia and Ecdysozoa 274

The Phylum Dicyemida (= Rhombozoa) 275

Anatomy and Biology of Dicyemidans 275

Life Cycles 277

## **CHAPTER 11** Gnathifera: The Phyla Gnathostomulida, Rotifera (including Acanthocephala), Micrognathozoa, and Chaetognatha 281

Phylum Gnathostomulida: The Gnathostomulids 283

The Gnathostomulid Body Plan 284

Body Wall, Support, and Locomotion 284

Nutrition, Circulation, Excretion,  
and Gas Exchange 284

Nervous System 284

Reproduction and Development 284

Phylum Rotifera: The Free-Living Rotifers 284

The Rotifer Body Plan 286

Body Wall, General External Anatomy,  
and the Corona 286

Body Cavity, Support, and Locomotion 287

Feeding and Digestion 288

Circulation, Gas Exchange, Excretion, and  
Osmoregulation 289

Nervous System and Sense Organs 290

Reproduction and Development 290

Phylum Rotifera, Subclass Acanthocephala:  
The Acanthocephalans 292

The Acanthocephalan Body Plan 293

Body Wall, Support, Attachment, and Nutrition 293

Circulation, Gas Exchange, and Excretion 294

Nervous System 294

Reproduction and Development 294

Phylum Micrognathozoa: The Micrognathozoans 295

The Micrognathozoan Body Plan 296

Epidermis, Ciliation, and Body Wall Musculature 296

Locomotion 298

Pharyngeal Apparatus, Feeding, and Digestion 298

Circulation, Gas Exchange, and Excretion 298

Nervous System and Sense Organs 301

Reproduction and Development 301

Phylum Chaetognatha 301

The Chaetognath Body Plan 304

Body Wall, Support, and Movement 304

Feeding and Digestion 306

Circulation, Gas Exchange, and Excretion 306

Nervous System and Sense Organs 306

Reproduction and Development 307

## **CHAPTER 12** **Platytrichoza and Two Enigmatic Phyla: Entoprocta and Cycliophora** 311

- Phylum Entoprocta: The Entoprocts 312
- The Entoproct Body Plan 314
  - Body Wall, Support, and Movement 314
  - Feeding and Digestion 314
- Circulation, Gas Exchange, and Excretion 314
- Nervous System 315
- Reproduction and Development 316
- Phylum Cycliophora: The Cycliophorans 317

## **CHAPTER 13** **Introduction to the Lophotrochozoa, and the Phylum Mollusca** 321

- Phylum Mollusca 322
- Taxonomic History and Classification 322
- The Molluscan Body Plan 344
  - The Body Wall 346
  - The Mantle and Mantle Cavity 346
  - The Molluscan Shell 347
  - Torsion, or “How the Gastropod Got its Twist” 353
  - Locomotion 356
  - Feeding 361
- Digestion 370
- Circulation and Gas Exchange 373
- Excretion and Osmoregulation 377
- Nervous System 378
- Sense Organs 380
- Cephalopod Coloration and Ink 384
- Reproduction 385
- Development 389
- Molluscan Evolution and Phylogeny 392

## **CHAPTER 14** **Phylum Nemertea: The Ribbon Worms** 397

- Taxonomic History and Classification 399
  - Classification 399
- The Nemertean Body Plan 400
  - Body Wall 401
  - Support and Locomotion 402
- Feeding and Digestion 402
- Circulation and Gas Exchange 406
- Excretion and Osmoregulation 406
- Nervous System and Sense Organs 408
- Reproduction and Development 409
- Nemertean Phylogeny 411

## **CHAPTER 15** **Phylum Annelida: The Segmented (and Some Unsegmented) Worms** 415

- Taxonomic History and Classification 416
- The Annelid Body Plan 426
  - Body Forms 426
  - Body Wall and Coelomic Arrangement 428
  - Support and Locomotion 429
  - Feeding and Digestion 432
  - Circulation and Gas Exchange 441
  - Excretion and Osmoregulation 444
  - Nervous System and Sense Organs 446
  - Reproduction and Development 450
- Sipuncula: The Peanut Worms 457
- Classification of Sipuncula 459
- The Sipunculan Body Plan 460
  - Body Wall, Coelom, Circulation, and Gas Exchange 460
  - Support and Locomotion 461
  - Feeding and Digestion 462
  - Excretion and Osmoregulation 462
  - Nervous System and Sense Organs 463
  - Reproduction and Development 463
- Thalassematidae: The Spoon Worms 465
  - Body Wall and Coelom 465
  - Support and Locomotion 465
  - Feeding and Digestion 465
  - Circulation and Gas Exchange 469
  - Excretion and Osmoregulation 469
  - Nervous System and Sense Organs 469
  - Reproduction and Development 469
- Siboglinidae: Vent Worms and Their Kin 470
- Siboglinid Taxonomic History 473
- The Siboglinid Body Plan 473
  - The Tube, Body Wall, and Body Cavity 473
  - Nutrition 474
  - Circulation, Gas Exchange, Excretion, and Osmoregulation 474
  - Nervous System and Sense Organs 474
  - Reproduction and Development 474
- Hirudinea: Leeches and Their Relatives 476

The Hirudinean Body Plan	477
Body Wall and Coelom	477
Support and Locomotion	477
Feeding and Digestion	478
Circulation and Gas Exchange	479

Excretion and Osmoregulation	480
Nervous System and Sense Organs	480
Reproduction and Development	481
Orthonectida: Extremely Simplified Annelids	482
Annelid Phylogeny	483

## **CHAPTER 16** The Lophophorates: Phyla Phoronida, Bryozoa, and Brachiopoda 487

Taxonomic History of the Lophophorates	488
The Lophophorate Body Plan	489
Phylum Phoronida: The Phoronids	490
The Phoronid Body Plan	490
Body Wall, Body Cavity, and Support	490
The Lophophore, Feeding, and Digestion	494
Circulation, Gas Exchange, and Excretion	494
Nervous System	495
Reproduction and Development	495
Phylum Bryozoa: The Moss Animals	496
The Bryozoan Body Plan	499
The Body Wall, Coelom, Muscles, and Movement	501

Zooid Interconnections	502
The Tentacle Crown, Feeding, and Digestion	503
Circulation, Gas Exchange, and Excretion	504
Nervous System and Sense Organs	505
Reproduction and Development	506
Phylum Brachiopoda: The Lamp Shells	509
The Brachiopod Body Plan	512
The Body Wall, Coelom, and Support	512
The Lophophore, Feeding, and Digestion	513
Circulation, Gas Exchange, and Excretion	514
Nervous System and Sense Organs	515
Reproduction and Development	515

## **CHAPTER 17** Rousphozoa: The Phyla Platyhelminthes (Flatworms) and Gastrotricha (Hairy-Bellied Worms) 519

Introduction to Rousphozoa	519
The Phylum Platyhelminthes (Flatworms)	520
Taxonomic History and Classification	522
The Platyhelminth Body Plan	527
Body Wall	529
Support, Locomotion, and Attachment	532
Feeding and Digestion	533
Circulation and Gas Exchange	537
Excretion and Osmoregulation	538
Nervous System and Sense Organs	539
Reproduction and Development	541

Platyhelminth Phylogeny	554
Phylum Gastrotricha: The Gastrotrichs, or Hairy-Bellied Worms	556
The Gastrotrich Body Plan	558
Body Wall	558
Support and Locomotion	558
Feeding and Digestion	558
Circulation, Gas Exchange, Excretion, and Osmoregulation	558
Nervous System and Sense Organs	558
Reproduction and Development	560

## **CHAPTER 18** Introduction to Ecdysozoa: Scalidophora (Phyla Kinorhyncha, Priapula, Loricifera) 563

Introduction to Ecdysozoa	563
The Scalidophora	564
Phylum Kinorhyncha: The Kinorhynchs, or Mud Dragons	564
The Kinorhynch Body Plan	567
Body Wall	567
Support and Locomotion	567
Feeding and Digestion	567
Circulation, Gas Exchange, Excretion, and Osmoregulation	567

Nervous System and Sense Organs	568
Reproduction and Development	568
Phylum Priapula: The Priapulans, or Penis Worms	568
Priapulan Body Plan	570
Body Wall, Support, and Locomotion	570
Feeding and Digestion	571
Circulation, Gas Exchange, Excretion, and Osmoregulation	571
Nervous System and Sense Organs	572
Reproduction and Development	572
Phylum Loricifera: The Loriciferans	572

**CHAPTER 19 Nematoida: Phyla Nematoda and Nematomorpha 579**

Phylum Nematoda: Roundworms 581  
 Classification of Phylum Nematoda 582  
 The Nematode Body Plan 586  
   Body Wall, Support, and Locomotion 586  
   Feeding and Digestion 588  
   Circulation, Gas Exchange, Excretion, and Osmoregulation 590  
   Nervous System and Sense Organs 592  
   Reproduction, Development, and Life Cycles 594  
 Life Cycles of Some Parasitic Nematodes 597

Phylum Nematomorpha: Horsehair Worms and Their Kin 600  
 The Nematomorph Body Plan 601  
   Body Wall, Support, and Locomotion 601  
   Feeding and Digestion 603  
   Circulation, Gas Exchange, Excretion, and Osmoregulation 603  
   Nervous System and Sense Organs 604  
   Reproduction and Development 604

**CHAPTER 20 Panarthropoda and the Emergence of the Arthropods: Tardigrades, Onychophorans, and the Arthropod Body Plan 607**

Phylum Tardigrada 610  
 The Tardigrade Body Plan 613  
   Locomotion 615  
   Feeding, Digestion, and Excretion 616  
   Circulation and Gas Exchange 616  
   Nervous System and Sense Organs 616  
   Reproduction and Development 617  
 Phylum Onychophora 619  
 The Onychophoran Body Plan 622  
   Locomotion 623  
   Feeding and Digestion 624  
   Circulation and Gas Exchange 624  
   Excretion and Osmoregulation 625  
   Nervous System, Sense Organs, and Behavior 625  
   Reproduction and Development 626  
   Systematics and Biogeography 628

An Introduction to the Phylum Arthropoda 628  
   Taxonomic History and Classification 629  
 The Arthropod Body Plan and Arthropodization 630  
   The Body Wall 632  
   Arthropod Appendages 634  
   Support and Locomotion 636  
   Growth 639  
   The Digestive System 642  
   Circulation and Gas Exchange 644  
   Excretion and Osmoregulation 646  
   Nervous System and Sense Organs 647  
   Reproduction and Development 651  
 The Evolution of Arthropods 652  
   The Origin of Arthropods 652  
   Evolution within the Arthropoda 652

**CHAPTER 21 Phylum Arthropoda—Subphylum Crustacea: Crabs, Shrimps, and Their Kin 659**

Classification of the Crustacea 663  
 Synopses of Crustacean Taxa 666  
 The Crustacean Body Plan 699  
   Locomotion 703  
   Feeding 708

Digestive System 714  
 Circulation and Gas Exchange 717  
 Excretion and Osmoregulation 719  
 Nervous System and Sense Organs 720  
 Reproduction and Development 724  
 Crustacean Phylogeny 730

## **CHAPTER 22** Phylum Arthropoda—Subphylum Hexapoda: Insects and Their Kin 735

- Classification of the Subphylum Hexapoda 738
- Synopses of Hexapod Groups 739
- The Hexapod Body Plan 751
  - General Morphology 751
  - Locomotion 758
  - The Origin of Insect Flight 761
- Feeding and Digestion 762
- Circulation and Gas Exchange 767
- Excretion and Osmoregulation 770
- Nervous System and Sense Organs 771
- Reproduction and Development 775
- Hexapod Evolution 780

## **CHAPTER 23** Phylum Arthropoda—Subphylum Myriapoda: Centipedes, Millipedes, and Their Kin 785

- Myriapod Classification 787
- The Myriapod Body Plan 789
  - Head and Mouth Appendages 791
  - Locomotion 791
  - Feeding and Digestion 791
- Circulation and Gas Exchange 793
- Excretion and Osmoregulation 794
- Nervous System and Sense Organs 794
- Reproduction and Development 795
- Embryonic Development 798
- Myriapod Phylogeny 798

## **CHAPTER 24** Phylum Arthropoda: Subphylum Chelicerata 801

- Synopses of Living Chelicerate Groups 807
- The Euchelicerate Body Plan 818
  - Spinnerets, Spider Silk, and Spider Webs 819
  - Locomotion 823
  - Feeding and Digestion 826
  - Circulation and Gas Exchange 831
  - Excretion and Osmoregulation 834
  - Nervous System and Sense Organs 834
  - Reproduction and Development 837
- The Class Pycnogonida 846
- The Pycnogonid Body Plan 849
  - External Anatomy 849
  - Locomotion 850
  - Feeding and Digestion 850
  - Circulation, Gas Exchange, and Excretion 852
  - Nervous System and Sense Organs 852
  - Reproduction and Development 852
- Chelicerate Phylogeny 854

## **CHAPTER 25** Introduction to Deuterostomia, and the Phylum Hemichordata 857

- Introduction to the Deuterostomia 857
- Phylum Hemichordata: Acorn Worms and Pterobranchs 859
- The Hemichordate Body Plan 862
- Class Enteropneusta (Acorn Worms) 863
  - External Anatomy 863
  - Support Structures 863
  - Coelomic Cavities 863
  - Musculature and Locomotion 865
  - Feeding and Digestion 865
  - Circulatory System 866
  - Excretory System 866
  - Gas Exchange 866
- Nervous System 866
- Reproduction and Development 866
- Class Pterobranchia (Pterobranchs) 868
  - Body Wall and Cavities 869
  - Support, Muscles, and Movement 869
  - Gut and Feeding 869
  - Circulation and Gas Exchange 869
  - Nervous System 870
  - Reproduction and Development 870
- Hemichordate Fossil Record and Phylogeny 870

## **CHAPTER 26** Phylum Echinodermata: Starfish, Sea Urchins, Sea Cucumbers, and their Kin 873

- Taxonomic History and Classification 877
- The Echinoderm Body Plan 881
  - Developmental Roots of the Echinoderm Body Plan 881
  - Body Wall and Coelom 883
  - Mutable Collagenous Tissue 885
  - Water Vascular System 885
  - Support and Locomotion 887
  - Feeding and Digestion 889
- Circulation and Gas Exchange 896
- Excretion and Osmoregulation 899
- Nervous System and Sense Organs 900
- Reproduction and Development 900
- Echinoderm Phylogeny 905**
  - First Echinoderms 905
  - Modern Echinoderms 908

## **CHAPTER 27** Phylum Chordata: Cephalochordata and Urochordata 911

- Phylum Chordata, Subphylum Cephalochordata:
  - The Lancelets 913
- The Cephalochordate Body Plan 913
  - Body Wall, Support, and Locomotion 913
  - Feeding and Digestion 915
  - Circulation, Gas Exchange, and Excretion 915
  - Nervous System and Sense Organs 916
  - Reproduction and Development 916
- Phylum Chordata, Subphylum Urochordata:
  - The Tunicates 917
- The Tunicate Body Plan 920
  - Body Wall, Support, and Locomotion 925
  - Feeding and Digestion 925
  - Circulation, Gas Exchange, and Excretion 927
  - Nervous System and Sense Organs 927
  - Reproduction and Development 927
- Chordate Phylogeny 931

## **CHAPTER 28** Perspectives on Invertebrate Phylogeny 935

- Illustration Credits** IC-1
- Selected References** SR-1
- Index** I-1