Contents

Preface xvii
Acknowledgments xix

1 Introduction 1

Where Did Invertebrates Come From? 4

The Dawn of Life 4

The Ediacaran Epoch and the Origin of Animals 5

The Paleozoic Era (570-250 mya) 6

The Mesozoic Era (250-65 mya) 7

The Cenozoic Era (65 mya-present) 7

Where Do Invertebrates Live? 9

Marine Habitats 9

Estuaries and Coastal Marshlands 13

Freshwater Habitats 13

Terrestrial Habitats 14

A Special Type of Environment: Symbiosis 14

Some Comments On Evolution 15

Microevolution 15

Macroevolution 16

A Final Introductory Message to the Reader

2 Classification, Systematics, and Phylogeny 23

Biological Classification 24 Nomenclature 24 Systematics 27 Important Concepts and Terms 28
Constructing Phylogenies and Classifications
31

3 Animal Architecture and the Bauplan Concept 41

Body Symmetry 43 Cellularity, Body Size, Germ Layers, and Body Cavities 46

Locomotion and Support 49

Ameboid Locomotion 50 Cilia and Flagella 50

Muscles and Skeletons 52

Feeding Mechanisms 56

Intracellular and Extracellular Digestion 56

Feeding Strategies 57

Excretion and Osmoregulation 66

Nitrogenous Wastes and Water Conservation 66 Osmoregulation and Habitat 67

Excretory and Osmoregulatory Structures 68

Circulation and Gas Exchange 71

Internal Transport 71

Circulatory Systems 71

Hearts and Other Pumping Mechanisms 73

Gas Exchange and Transport 73

Nervous Systems and Sense Organs 77

Invertebrate Sense Organs 77 Sense Organs 78 Independent Effectors 82

Bioluminescence 82

Nervous Systems and Body Plans 82

Hormones and Pheromones 84 Reproduction 84

Asexual Reproduction 85 Sexual Reproduction 86 Parthenogenesis 88



4

Animal Development, Life Histories, and Origins 93

Eggs and Embryos 93

Eggs 94

Cleavage 94

The Problem of Cell Fates 98

Blastula Types 98

Gastrulation and Germ Layer Formation 99

Mesoderm and Body Cavities 100

Life Cycles: Sequences and Strategies 102

Classification of Life Cycles 102

Indirect Development 103

Settling and Metamorphosis 104

Direct Development 105

Mixed Development 105

Adaptations to Land and Fresh Water 106

Parasite Life Cycles 106

The Relationships between Ontogeny and Phylogeny 106

The Concept of Recapitulation 107 Heterochrony and Paedomorphosis 108

Origins of Major Groups of Metazoa 108

Origin of the Metazoa 108

Origin of the Bilateral Condition 112

Origin of the Coelomic Condition 112

5

The Protists 121

Taxonomic History and Classification 123 Classification of the Protista 123 The Protist Bauplan 124

Body Structure, Excretion, and Gas Exchange 124 Support and Locomotion 125

Nutrition 125

Activity and Sensitivity 125

Reproduction 127

Phylum Euglenida 129

Support and Locomotion 130

Nutrition 131

Reproduction 131

Phylum Kinetoplastida (The Trypanosomes and Their Relatives) 131

Support and Locomotion 133

Nutrition 134

Reproduction and Life Cycles 135

Phylum Ciliophora (The Ciliates) 135

Support and Locomotion 135

Nutrition 139

Reproduction 142

Phylum Apicomplexa (The Gregarines, Coccidians, Haemosporidians, and Piroplasms) 145

Support and Locomotion 146

Nutrition 146

Reproduction and Life Cycles 147

Phylum Dinoflagellata 148

Support and Locomotion 151

Nutrition 151

Reproduction 152

Phylum Stramenopila 153

Support and Locomotion 154 Nutrition 154

Reproduction 155

Phylum Rhizopoda (Amebas) 155

Support and Locomotion 157

Nutrition 159 Reproduction 160

Phylum Actinopoda 161

Support and Locomotion 162

Nutrition 163 Reproduction 164

Phylum Granuloreticulosa (Foraminifera and Their Kin) 165

Support and Locomotion 166

Nutrition 166 Reproduction and Some Life Cycles 167

Phylum Diplomonadida 167

Support and Locomotion 168

Nutrition 169 Reproduction 169

Phylum Parabasilida (The Trichomonads and Hypermastigotes) 169

Support and Locomotion 170

Nutrition 171

Reproduction 171

Phylum Cryptomonada 172

Phylum Microspora 172

Phylum Ascetospora 173

Phylum Choanoflagellata 173

Phylum Chlorophyta 173

Phylum Opalinida 173

Genus Stephanopogon 174

Protist Phylogeny 174

6

Phylum Porifera: The Sponges 179

Taxonomic History and Classification 180 The Poriferan Bauplan 182

Body Structure and the Aquiferous System 183

Cell Types 188

Cell Aggregation 191

Support 191

Nutrition, Excretion, and Gas Exchange 192

Activity and Sensitivity 194

Reproduction and Development 196

Some Additional Aspects of Sponge Biology 201

Distribution and Ecology 201 Biochemical Agents 201 Growth Rates 202 Symbioses 202

Poriferan Phylogeny 203

The Origin of Sponges 203 Evolution within the Porifera 204





Four Phyla of Uncertain Affinity 209

Taxonomic History 209 Mesozoan Bauplans 210

Phylum Placozoa 210 Phylum Monoblastozoa 210 Phylum Rhombozoa 211 Phylum Orthonectida 215 **Mesozoan Phylogeny 216**

Phylum Cnidaria 219



Taxonomic History and Classification 222 The Cnidarian Bauplan 225

The Body Wall 226 Support 236 Movement 239 Cnidae 242 Feeding and Digestion 244 Defense, Interactions, and Symbiosis 246 Circulation, Gas Exchange, Excretion, and Osmoregulation 250 Nervous System and Sense Organs 250 Reproduction and Development 253 Cnidarian Phylogeny 261

Phylum Ctenophora: The Comb Jellies 269

Taxonomic History and Classification 271 The Ctenophoran Bauplan 274

Support and Locomotion 274 Feeding and Digestion 276

Circulation, Excretion, Gas Exchange, and Osmoregulation 279 Nervous System and Sense Organs 279 Reproduction and Development 280 Ctenophoran Phylogeny 281

Phylum Platyhelminthes 285

Taxonomic History and Classification 286 The Platyhelminth Bauplan 289

Body Wall 291 Support, Locomotion, and Attachment 294 Feeding and Digestion 295

Circulation and Gas Exchange 299 Excretion and Osmoregulation 299 Nervous System and Sense Organs 300 Reproduction and Development 303 Platyhelminth Phylogeny 313

Phylum Nemertea: The Ribbon Worms 319

Taxonomic History and Classification 321 Classification 321

The Nemertean Bauplan 322

Body Wall 322 Support and Locomotion 322 Feeding and Digestion 323

Circulation and Gas Exchange 327 Excretion and Osmoregulation 328 Nervous System and Sense Organs 329 Reproduction and Development 331

Nemertean Phylogeny 333

12 Blastocoelomates and Other Phyla 337

Taxonomic History 338 The Blastocoelomate Condition 338 Phylum Rotifera:

The Rotifers 338

General External Anatomy and Details of the Corona 340

Body Wall, Body Cavity, Support, and Locomotion 341

Feeding and Digestion 341

Circulation, Gas Exchange, Excretion, and Osmoregulation 343

Nervous System and Sense Organs 343 Reproduction and Development 343

Phylum Gastrotricha:

The Gastrotrichs 345

Body Wall, Support, and Locomotion 346 Feeding and Digestion 347

Circulation, Gas Exchange, Excretion, and Osmoregulation 347

Nervous System and Sense Organs 347 Reproduction and Development 347

Phylum Kinorhyncha: The Kinorhynchs 348

Body Wall 349

Support and Locomotion 350

Feeding and Digestion 350

Circulation, Gas Exchange, Excretion, and Osmoregulation 350

Nervous System and Sense Organs 350 Reproduction and Development 350

Phylum Nemata:

The Nematodes 351

Body Wall, Support, and Locomotion 352 Feeding and Digestion 353

Circulation, Gas Exchange, Excretion, and Osmoregulation 355

Nervous System and Sense Organs 357 Reproduction, Development, and Life Cycles 357 Life Cycles of Some Parasitic Nematodes 359

Phylum Nematomorpha: Hair Worms and Their Kin 362

Body Wall, Support, and Locomotion 363 Feeding and Digestion 363 Circulation, Gas Exchange, Excretion, and Osmoregulation 363

Nervous System and Sense Organs 365 Reproduction and Development 365

Phylum Priapula: The Priapulans 365

Body Wall, Support, and Locomotion 367 Feeding and Digestion 367

Circulation, Gas Exchange, Excretion, and Osmoregulation 368

Nervous System and Sense Organs 368 Reproduction and Development 368

Phylum Acanthocephala: The Acanthocephalans 368

Body Wall, Support, Attachment, and Nutrition 369

Circulation, Gas Exchange, and Excretion 370 Nervous System 370 Reproduction and Development 370

Phylum Entoprocta: The Entoprocts 371

Body Wall, Support, and Movement 373 Feeding and Digestion 373 Circulation, Gas Exchange, and Excretion 374 Nervous System 374 Reproduction and Development 374

Phylum Gnathostomulida: The Gnathostomulids 375

Body Wall, Support, and Locomotion 376 Nutrition, Circulation, Excretion, and Gas Exchange 376

Nervous System 377

Reproduction and Development 377

Phylum Loricifera:

The Loriciferans 377

Phylum Cycliophora: The Cycliophorans 378

Some Phylogenetic Considerations 381



13 Phylum Annelida: The Segmented Worms 387



Taxonomic History and Classification 388 The Annelid Bauplan 395

Body Forms 395
Body Wall and Coelomic Arrangement 397
Support and Locomotion 400
Feeding 405
Digestive System 410

Circulation and Gas Exchange 413 Excretion and Osmoregulation 417 Nervous System and Sense Organs 420 Regeneration and Asexual Reproduction 425 Sexual Reproduction and Development 427

Siboglinidae: The Beard Worms 434

Taxonomic History 434
The Tube, Body Wall, and Body Cavity 434
Nutrition 436
Circulation, Gas Exchange, Excretion, and
Osmoregulation 436
Nervous System and Sense Organs 437
Reproduction and Development 437

Annelid Phylogeny 438

14 Sipuncula and Echiura 445

The Sipunculans 445

Taxonomic History and Classification 447

The Sipunculan Bauplan 447

Body Wall, Coelom, Circulation, and Gas Exchange 447 Support and Locomotion 449 Feeding and Digestion 449 Excretion and Osmoregulation 450 Nervous System and Sense Organs 450 Reproduction and Development 451

The Echiurans 451

Taxonomic History and Classification 452

The Echiuran Bauplan 453

Body Wall and Coelom 453
Support and Locomotion 453
Feeding and Digestion 454
Circulation and Gas Exchange 455
Excretion and Osmoregulation 456
Nervous System and Sense Organs 456
Reproduction and Development 456

Some Comments on Phylogeny 457

The Emergence of the Arthropods: Onychophorans, Tardigrades, Trilobites, and the Arthropod Bauplan 461

Phylum Onychophora 463 Phylum Tardigrada 469 An Introduction to the Arthropods 475

Taxonomic History and Classification 475
Synopses of the Five Arthropod Subphyla 476
The Arthropod Bauplan and Arthropodization 476
The Body Wall 478
Arthropod Appendages 479
Support and Locomotion 482
Growth 485
The Digestive System 489
Circulation and Gas Exchange 489

Excretion and Osmoregulation 491 Nervous System and Sense Organs 492 Reproduction and Development 495

The Trilobites (Subphylum Trilobitomorpha) 497

General Body Form 497 Internal Anatomy 499 Development 499

The Evolution of Arthropods 499

The Origin of the Arthropoda 499 Evolution within the Arthropoda 500 Emerging Views of Arthropod Relationships 503 Where Are We Now? 506

16 Phylum Arthropoda: The Crustacea 511



Classification of the Crustacea 514 Subphylum Crustacea 514

Synopses of Crustacean Taxa 517 The Crustacean Bauplan 550

Locomotion 551
Feeding 557
Digestive System 561
Circulation and Gas Exchange 563
Excretion and Osmoregulation 568
Nervous System and Sense Organs 570
Reproduction and Development 573

Crustacean Phylogeny 579

17 Phylum Arthropoda: The Hexapoda (Insects and Their Kin) 589

Hexapod Classification 593
Subphylum Hexapoda 594
Synopses of Major Hexapod Taxa 594
The Hexapod Bauplan 601

General Morphology 601 Locomotion 607 Feeding and Digestion 610 Circulation and Gas Exchange 617 Excretion and Osmoregulation 618 Nervous System and Sense Organs 619 Reproduction and Development 623

Hexapod Evolution 628

The Origin of the Hexapoda 628 The Origin of Insect Flight 629 Evolution within the Hexapoda 630



18 Phylum Arthropoda: The Myriapods (Centipedes, Millipedes, and Their Kin) 637

Myriapod Classification 639
Subphylum Myriapoda 639
Synopses of Myriapod Taxa 639
The Myriapod Bauplan 640

Head and Mouth Appendages 642 Locomotion 642 Feeding and Digestion 644
Circulation and Gas Exchange 644
Excretion and Osmoregulation 646
Nervous System and Sense Organs 646
Reproduction and Development 647
Myriapod Embryogeny 649
Myriapod Phylogeny 649

19 Phylum Arthropoda: The Cheliceriformes 653

Subphylum Cheliceriformes 654 Synopses of the Chelicerate Taxa 656 The Chelicerate Bauplan 666

Spinnerets, Spider Silk, and Spider "Webs" 667
Locomotion 670
Feeding and Digestion 672
Circulation and Gas Exchange 678
Excretion and Osmoregulation 679
Nervous System and Sense Organs 680
Reproduction and Development 683

The Class Pycnogonida 691 The Pycnogonid Bauplan 692

External Anatomy 692 Locomotion 695 Feeding and Digestion 695 Circulation, Gas Exchange, and Excretion 695 Nervous System and Sense Organs 696 Reproduction and Development 696

Cheliceriform Phylogeny 696

20 Phylum Mollusca 701

Taxonomic History and Classification 702 The Molluscan Bauplan 715



The Body Wall 718
The Mantle and Mantle Cavity 719
The Molluscan Shell 720
Torsion, or "How the Gastropod Got Its Twist" 725
Locomotion 728
Feeding 733
Digestion 741
Circulation and Gas Exchange 744
Excretion and Osmoregulation 747
Nervous System 748
Sense Organs 752
Cephalopod Coloration and Ink 754
Reproduction 755
Development 759

Molluscan Evolution and Phylogeny 761

21 Lophophorates 771

The Lophophorates: An Overview 771
Taxonomic History 772
The Lophophorate Bauplan 773
Phylum Phoronida 773
The Phoronid Bauplan 774

Body Wall, Body Cavity, and Support 775
The Lophophore, Feeding, and Digestion 776
Circulation, Gas Exchange, and Excretion 776
Nervous System 777
Reproduction and Development 777

Phylum Ectoprocta 778 The Ectoproct Bauplan 779

The Body Wall, Coelom, Muscles, and Movement 783

Zooid Interconnections 785 The Lophophore, Feeding, and Digestion 785 Circulation, Gas Exchange, and Excretion 788 Nervous System and Sense Organs 788 Reproduction and Development 789

Phylum Brachiopoda 792 The Brachiopod Bauplan 793

The Body Wall, Coelom, and Support 793
The Lophophore, Feeding, and Digestion 795
Circulation, Gas Exchange, and Excretion 796
Nervous System and Sense Organs 796
Reproduction and Development 796

Lophophorate Phylogeny 798

22 Phylum Echinodermata 801

Taxonomic History and Classification 803 The Echinoderm Bauplan 806

Body Wall and Coelom 808 Water Vascular System 810 Support and Locomotion 813 Feeding and Digestion 814 Circulation and Gas Exchange 823
Excretion and Osmoregulation 824
Nervous System and Sense Organs 825
Reproduction and Development 826

Echinoderm Phylogeny 830

23 Other Deuterostomes: Chaetognatha, Hemichordata, Chordata 839

Taxonomic History and Classification 839
Phylum Chaetognatha: Arrow Worms 841
The Chaetognath Bauplan 841
Phylum Hemichordata:
 The Hemichordates 847
The Hemichordate Bauplan 849
Phylum Chordata: The Chordates 854
The Urochordates (Tunicates) 855
The Tunicate Bauplan 857
The Cephalochordates 864
The Cephalochordate Bauplan 865
Phylogenetic Considerations 868



24 Perspectives on Invertebrate Phylogeny 873

A Word about Characters 876 Metazoan Evolution 876

The Tree 876 Metazoan Roots 876 Evolution within the Metazoa 877 Other Ideas about Animal Phylogeny 882
Molecular Phylogenetics 882
Evolutionary Developmental Biology 884



Appendix A: Common Human Diseases
Transmitted by Insects 890

Appendix B: Data Matrix for Analysis of
Metazoan Phylogeny 892

Illustration Credits 897

Index 903