

Contents

PREFACE xv

ACKNOWLEDGMENTS xvii

1 INTRODUCTION TO INVERTEBRATES 1

RECONSTRUCTION OF INVERTEBRATE
PHYLOGENY 1

Cladistic Method 1

Downplaying the Linnean Categories 4

AN EXERCISE IN CLADISTICS 4

REFERENCES 8

2 INTRODUCTION TO PROTOZOA 11

EUKARYOTIC CELL STRUCTURE 12

Cell Motility 14

Uptake by Cells 17

Intracellular Digestion 17

Circulation in Cells 17

Cell Secretions 18

Cell Communication 19

Symbiosis Between Cells 19

EVOLUTIONARY ORIGIN OF EUKARYOTIC CELLS
(INCLUDING PROTOZOA) 19

REFERENCES 21

3 PROTOZOA 22

FORM AND FUNCTION 23

REPRODUCTION AND LIFE CYCLES 25

DIVERSITY OF PROTOZOA 27

Euglenozoa^P 27

Chlorophyta^P 30

Choanoflagellata^P 30

Retortamonada^P and Axostylata^P 31

Alveolata^P 32

Ameboid Protozoa 46

PHYLOGENY OF PROTOZOA 54

REFERENCES 55

4 INTRODUCTION TO METAZOA 58

GROUND PLAN 59

Cells, Tissues, and Skeletons 59

Reproduction and Development 60

FUNCTIONAL CONSEQUENCES
OF BODY SIZE 62

Size and Compartmentalization 63

Size, Surface Area, and Volume 63

Size and Transport 65

Size and Metabolism 65

Advantages of Large Body Size 67

ONTOGENY AND PHYLOGENY 67

EVOLUTIONARY ORIGINS 70

Origin of Metazoa 70

Origin of Polarity and Cell Specialization 71

Origin of Complexity 73

REFERENCES 75

5 PORIFERA^P AND PLACOZOA^P 76

PORIFERA^P 77

Form 78

Body Wall 80

Water Pumping 83

Skeleton 83

Locomotion and Dynamic Tissues 85

Physiological Compartmentalization 87

Nutrition 87

Internal Transport, Gas Exchange,
and Excretion 88

Integration 89

Bioactive Metabolites and Biological
Associations 89

Bioerosion 89

Reproduction 90

Diversity of Porifera 92

Paleontology and Phylogeny of Porifera 93

PLACOZOA^P 94

REFERENCES 96

6 INTRODUCTION TO EUMETAZOA 98

EPITHELIAL TISSUE 99

EPIDERMIS, GASTRODERMIS,
AND GUT 100

CONNECTIVE TISSUE 100

SKELETONS 101

Fluid Skeleton 101

Solid Skeleton 102

MOVEMENT AND BODY SIZE 102

MUSCLE CELLS AND TISSUE
(MUSCULATURE) 103NERVE CELLS (NEURONS) AND TISSUE
(NERVOUS SYSTEM) 104

SENSE CELLS AND ORGANS 105

Form and Function 105

Gravity Receptors 107

Photoreceptors and Eyes 107

DEVELOPMENT 107

GROWTH 108

REFERENCES 109

7 CNIDARIA^P 111

GENERAL BIOLOGY 112

Form and Symmetry of Solitary
Individuals 112

Form of Colonial Individuals 114

Skeleton 116

Musculature and Movement 116

Nervous System 117

Cnidocytes and Cnidae 119

Interstitial Cells 121

Coelenteron: Nutrition and
Internal Transport 121

Gas Exchange and Excretion 122

Reproduction and Development 122

ANTHOZOA^C 124

Polyp Form 124

Musculature and Nervous System 126

Retraction and Extension 127

Nutrition and Internal Transport 128

Gas Exchange and Excretion 130

Reproduction and Growth 130

Diversity of Anthozoa 130

Phylogeny of Anthozoa 146

MEDUSOZOA 148

Scyphozoa^C 148Hydrozoa^C 156

PHYLOGENY OF CNIDARIA 175

REFERENCES 176

8 CTENOPHORA^P 181

GENERAL BIOLOGY 183

Body Wall and Collocytes 184

Musculature 185

Nervous System 186

Locomotion 187

Coelenteron 187

Prey Capture, Digestion, Internal Transport 188

Excretion and Buoyancy Regulation 189

Reproduction and Development 189

DIVERSITY OF CTENOPHORA 191

PHYLOGENY OF CTENOPHORA 194

REFERENCES 195

9 INTRODUCTION TO BILATERIA 196BILATERAL SYMMETRY—ENCOUNTERING
RESOURCES 197

CEPHALIZATION—TARGETING RESOURCES 199

Motile Bilateria 199

Sessile Bilateria 200

MUSCULATURE—PURSUING RESOURCES 200

BURROWING MECHANICS 201

COMPARTMENTALIZATION—PHYSIOLOGICAL
REGULATION AND SPECIALIZATION 202

Cnidaria 202

Bilateria 203

INTERNAL TRANSPORT 207

Large Bilateria 207

Small Bilateria 209

GAS EXCHANGE AND RESPIRATORY
PIGMENTS 210

Large Bilateria 210

Small Bilateria 211

EXCRETION 212

General 212

Large Bilateria 212

Small Bilateria 213

REPRODUCTION AND DEVELOPMENT 214

- Sexual Reproduction 214
- Cleavage Patterns and Developmental Determinism 216
- Gastrulation 217
- Mesoderm Segregation 217
- Fates of the Blastopore 219

PHYLOGENY OF BILATERIA 219

- Consensus and Conflicts 219
- The Ancestor: Small or Large? 221

REFERENCES 223

10 PLATYHELMINTHES^P, ORTHONECTIDA^P, AND DICYEMIDA^P 225

- PLATYHELMINTHES^P 226
- Turbellaria^C 227
- Neodermata 249
- "MESOZOA" 263
- Orthonectida^P 264
- Dicyemida^P 265
- Phylogeny of Orthonectida and Dicyemida 266

REFERENCES 266

11 NEMERTEA^P 270**GENERAL BIOLOGY 271**

- Form 271
- Body Wall, Locomotion, and Extensibility 272
- Proboscis and Rhynchocoel 273
- Nutrition and Digestive System 274
- Gas Exchange, Internal Transport, and Excretion 275
- Nervous System and Sense Organs 276
- Reproduction and Development 276
- Functional Design of Nemertea 278

DIVERSITY OF NEMERTEA 279**PHYLOGENY OF NEMERTEA 279****REFERENCES 280**

12 MOLLUSCA^P 283**GENERALIZED MOLLUSC 284**

- Mantle 284
- Shell 284
- Mantle Cavity 284

- Gills 286
- Osphradia 286
- Foot 286
- Nutrition 286
- Coelom 288
- Internal Transport 288
- Excretion 289
- Nervous System and Sense Organs 289
- Reproduction 289
- Development 289

APLACOPHORA^C 291

- Form 291
- Diversity of Aplacophora 292

POLYPLACOPHORA^C 292

- Mantle 292
- Shell 293
- Foot and Locomotion 294
- Mantle Cavity and Ventilation 295
- Nutrition 295
- Internal Transport 296
- Excretion 296
- Nervous System and Sense Organs 296
- Reproduction and Development 297
- Diversity of Polyplacophora 298

MONOPLACOPHORA^C 298**GASTROPODA^C 300**

- Preview of Gastropod Systematics 300
- Origin and Evolution of the Gastropod Design 301
- Shell 309
- Foot, Locomotion, and Habitat 313
- Nutrition and Digestion 316
- Excretion 328
- Internal Transport 330
- Nervous System 331
- Sense Organs 331
- Reproduction 333
- Development 335
- Diversity and Evolution of Gastropoda 338

CEPHALOPODA^C 343

- Form 343
- Shell 344
- Locomotion 351
- Adaptive Diversity 353
- Nutrition 355

Gas Exchange 357
 Internal Transport 358
 Excretion 358
 Nervous System 360
 Sense Organs 360
 Integument and Chromatic Organs 362
 Reproduction 363
 Development 364
 Diversity of Cephalopoda 365
 Phylogeny of Cephalopoda 366

BIVALVIA^C 367

Form 367
 Mantle 368
 Shell 368
 Foot 371
 Gills and the Evolution of
 Bivalve Feeding 372
 Nutrition 380
 Adaptive Radiation of
 Lamellibranchs 382
 Internal Transport 396
 Gas Exchange 396
 Excretion 396
 Nervous System 396
 Sense Organs 397
 Reproduction 398
 Development 398
 Diversity of Bivalvia 401
 Phylogeny of Bivalvia 402

SCAPHOPODA^C 403

Form 403
 Mantle and Mantle Cavity 404
 Shell 404
 Nutrition 405
 Internal Transport 405
 Excretion 405
 Nervous System and
 Sense Organs 405
 Reproduction and Development 405
 Diversity of Scaphopoda 406
 Phylogeny of Scaphopoda 406

PHYLOGENY OF MOLLUSCA 407

Molluscan Ground Plan 407
 Origin of Mollusca 407
 Evolution Within Mollusca 407

REFERENCES 408

13 ANNELIDA^P 413

FORM AND FUNCTION 414

Segmentation 414
 Body Wall 414
 Nervous System 416
 Coelom and Hemal System 417
 Excretory System 419
 Digestive System 419
 Reproduction and Development 419

DIVERSITY OF ANNELIDA 419

PHYLOGENY OF ANNELIDA 419

**EVOLUTION AND SIGNIFICANCE OF
 SEGMENTATION 420**

POLYCHAETA^C 422

Form and Function 422
 Body Wall and Tubes 423
 Musculature and Locomotion 423
 Nervous System and
 Sense Organs 425
 Digestive System 428
 Nutrition 428
 Gas Exchange 430
 Internal Transport 431
 Excretion 434
 Reproduction 434
 Diversity of Polychaeta 441
 Phylogeny of Polychaeta 457

CLITELLATA 459

Oligochaeta^C 459
 Hirudinomorpha^C 471
 Phylogeny of Clitellata 482

REFERENCES 483

14 ECHIURA^P AND SIPUNCULA^P 489

ECHIURA^P 490

Form and Function 490
 Reproduction and Development 493
 Diversity of Echiura 494
 Phylogeny of Echiura 495

SIPUNCULA^P 495

Form and Function 495
 Reproduction and Development 499

Diversity of Sipuncula 500
Phylogeny of Sipuncula 500

REFERENCES 501

-
- 15 ONYCHOPHORA^P AND TARDIGRADA^P 504**
PANARTHROPODA^{SP} 505
ONYCHOPHORA^P 505
 Form 506
 Body Wall and Locomotion 506
 Nutrition 507
 Internal Transport, Gas Exchange, and Excretion 508
 Nervous System and Sense Organs 508
 Reproduction and Development 509
 Diversity of Onychophora 509
 Phylogeny of Onychophora 509
- TARDIGRADA^P 510**
 Form 510
 Body Wall 511
 Musculature and Locomotion 511
 Body Cavity 512
 Nutrition 512
 Gas Exchange and Excretion 514
 Nervous System and Sense Organs 514
 Reproduction and Development 514
 Diversity of Tardigrada 514
 Phylogeny of Tardigrada 515
- REFERENCES 515

-
- 16 INTRODUCTION TO ARTHROPODA^P 517**
FORM 518
 Segmentation 518
 Tagmosis 518
 Cephalization 520
 Segmental Appendages 520
- BODY WALL 521**
 Cilia and Flagella 521
 Exoskeleton 521
- MUSCULATURE AND MOVEMENT 525**
 Functional Morphology 525
 Physiology 526

COELOM AND MESODERM 527
INTERNAL TRANSPORT 527
EXCRETION 528
GAS EXCHANGE 530
NUTRITION 530
NERVOUS SYSTEM 531
SENSE ORGANS 532
 Exoreceptors 532
 Endoreceptors 537

REPRODUCTION 537
DEVELOPMENT 538
PHYLOGENY OF ARTHROPODA 539
REFERENCES 541

-
- 17 TRILOBITOMORPHA^{SP} 543**
FORM 544
DEVELOPMENT 547
ECOLOGY 548
DIVERSITY OF TRILOBITOMORPHA 550
PHYLOGENY OF TRILOBITOMORPHA 552
REFERENCES 553

-
- 18 CHELICERATA^{SP} 554**
FORM 555
XIPHOSURA^C 555
 Form 555
 Nutrition 556
 Internal Transport 558
 Gas Exchange 558
 Excretion 558
 Nervous System and Sense Organs 558
 Reproduction and Development 559
- ARACHNIDA^C 559**
 Form 560
 Nutrition 560
 Gas Exchange 560
 Internal Transport 561
 Excretion 561
 Nervous System and Sense Organs 562
 Reproduction and Development 564
 Eurypterida^O 564
 Scorpiones^O 565

Uropygi^O 569
 Amblypygi^O 570
 Araneae^O 571
 Palpigradi^O 584
 Pseudoscorpiones^O 584
 Solifugae^O 586
 Opiliones^O 588
 Ricinulei^O 590
 Acari^O 590
 Phylogeny of Arachnida 595

PYCNOGONIDA^C 597
 Form 597
 Internal Form and Function 598

PHYLOGENY OF CHELICERATA 600
REFERENCES 601

19 CRUSTACEA^{SP} 605
GENERAL BIOLOGY 606
 Form 606
 Nutrition 608
 Internal Transport 611
 Gas Exchange 612
 Excretion 612
 Nervous System and Sense Organs 613
 Reproduction 614
 Development 614

REMIPEDIA^C 615
CEPHALOCARIDA^C 616
ANOSTRACA^C 617
PHYLLOPODA^C 619
 Locomotion 619
 Nutrition 619
 Gas Exchange, Internal Transport,
 and Excretion 620
 Reproduction and Development 620
 Notostraca^O 623
 Laevicaudata^O and Spinicaudata^O 623
 Cladocera^{SO} 623
 Phylogeny of Phyllopoda 624

MALACOSTRACA^C 625
 Leptostraca^O 626
 Stomatopoda^O 627
 Decapoda^O 628
 Syncarida^{SO} 650

Euphausiacea^O 651
 Pancarida^{SO} 651
 Peracarida^{SO} 652
 Phylogeny of Malacostraca 668

MAXILLOPODA^{SC} 669
 Copepoda^C 669
 Mystacocarida^C 674
 Tantulocarida^C 675
 Ascothoracida^C 676
 Cirripedia^C 678
 Ostracoda^C 687
 Branchiura^C 690
 Pentastomida^C 691
 Phylogeny of Maxillopoda 692

PHYLOGENY OF CRUSTACEA 694
REFERENCES 695

20 MYRIAPODA^{SC} 702
TRACHEATA^{IP} AND MYRIAPODA^{SC} 703
 Chilopoda^C 703
 Symphyla^C 710
 Diplopoda^C 711
 Pauropoda^C 718

PHYLOGENY OF TRACHEATA 718
REFERENCES 721

21 HEXAPODA^{SC} 723
GENERAL BIOLOGY 724
 Form 724
 Wings and Flight 726
 Nutrition 727
 Internal Transport 732
 Gas Exchange 733
 Excretion 735
 Nervous System 735
 Sense Organs 735
 Reproduction 736
 Development 738

ECOLOGY 740
 Coevolution 740
 Parasitism 741
 Parasitoidism 742

- Communication 743
Social Insects 743
- DIVERSITY OF HEXAPODA 745
REFERENCES 750
-
- 22** CYCLONEURALIA^{SP} 752
GASTROTRICHA^P 753
Diversity of Gastrotricha 757
- NEMATODA^P 757
Form 757
Body Wall 757
Nervous System and Sense Organs 759
Locomotion 761
Nutrition 762
Excretion 763
Reproduction and Development 764
Parasitism 766
Diversity of Nematoda 769
- NEMATOMORPHA^P 770
Diversity of Nematomorpha 772
- PRIAPULIDA^P 772
Diversity of Priapulida 775
- LORICIFERA^P 776
Diversity of Loricifera 776
- KINORHYNCHA^P 778
Diversity of Kinorhyncha 779
- PHYLOGENY OF CYCLONEURALIA 779
REFERENCES 781
-
- 23** GNATHIFERA^{SP} 784
GNATHOSTOMULIDA^P 785
Diversity of Gnathostomulida 786
- MICROGNATHOZOA 786
SYNDERMATA 788
Rotifera^P 789
Seisonida^C 799
Acanthocephala^P 800
- PHYLOGENY OF GNATHIFERA 804
REFERENCES 805
-
- 24** KAMPTOZOA^P AND CYCLIOPHORA^P 807
KAMPTOZOA^P 808
Form 809
Internal Form and Function 810
Phylogeny of Kamptozoa 811
Diversity of Kamptozoa 811
- CYCLIOPHORA^P 812
Form 812
Reproduction and Life Cycles 813
Ecology 814
Phylogeny of Cyclophora 815
- REFERENCES 815
-
- 25** LOPHOPHORATA^{SP} 816
PHORONIDA^P 817
BRACHIOPODA^P 821
Form 824
Lophophore and Feeding 826
Internal Form and Function 826
Reproduction and Development 828
Diversity of Brachiopoda 829
- BRYOZOA^P 829
Form 830
Colony Forms 832
Zooid Polymorphism 834
Interzooidal Pores 836
Funicular System 837
Musculature 837
Nutrition 837
Gas Exchange, Internal Transport, Nervous System 839
Excretion 840
Reproduction and Development 840
Diversity of Bryozoa 844
Phylogeny of Bryozoa 845
- PHYLOGENY OF LOPHOPHORATA 846
REFERENCES 847
-
- 26** CHAETOGNATHA^P 850
FORM AND FUNCTION 851
REPRODUCTION AND DEVELOPMENT 855
PHYLOGENY OF CHAETOGNATHA 856
REFERENCES 856

27 INTRODUCTION TO DEUTEROSTOMIA
AND HEMICHORDATA^P 857

ENTEROPNEUSTA^C 858

Form 858

Coeloms, Musculature,
and Locomotion 859

Skeleton 859

Digestive System and Nutrition 861

Gas Exchange 861

Internal Transport and Excretion 863

Nervous System 863

Reproduction and Development 864

PTEROBRANCHIA^C 865

Zooid Form and Function 865

Colony Form and Locomotion 866

Body Wall and Internal Form 867

Digestive System and Nutrition 867

Reproduction and Development 867

PHYLOGENY OF HEMICHORDATA
AND DEUTEROSTOMIA 868

REFERENCES 870

28 ECHINODERMATA^P 872

GENERAL BIOLOGY 873

DEVELOPMENTAL ORIGIN OF PENTAMEROUS
SYMMETRY 875

ELEUTHEROZOA 876

Asteroidea^C 876

Cryptosyringida 889

CRINOIDEA^C 917

Form 917

Body Wall 917

Musculature and Locomotion 918

Digestive System and Nutrition 919

WVS and Internal Transport 920

Gas Exchange and Excretion 922

Nervous System 922

Reproduction 922

Development 922

Diversity of Crinoidea 924

PALEONTOLOGY AND PHYLOGENY
OF ECHINODERMATA 924

REFERENCES 926

29 CHORDATA^P 930

GROUND PLAN OF CHORDATA 931

CEPHALOCHORDATA^{SP} 932

Form and Locomotion 932

Nervous System and Sense Organs 935

Musculature and Notochord 935

Coelom 936

Digestive System and Nutrition 936

Hemal System and Internal Transport 937

Excretion 938

Reproduction and Development 939

Diversity of Cephalochordata 939

TUNICATA^{SP} (UROCHORDATA) 940

Ascidiacea^C 940

Thaliacea^C 952

Appendicularia^C (Larvacea) 955

PHYLOGENY OF CHORDATA 956

REFERENCES 960

INDEX I-1