
ON THE ORIGIN OF

PHYLA

JAMES W. VALENTINE

Universitäts- und Landes-
bibliothek Darmstadt
Bibliothek Biologie

Inv.-Nr. 16683
.....

The University of Chicago Press *Chicago and London*

Contents

Preface xxiii

PART ONE *Evidence of the Origins of Metazoan Phyla*

I

I The Nature of Phyla 7

Phyla Are Morphologically Based Branches of the Tree of Life 7

Concepts of Animal Phyla Have Developed over Hundreds of Years 7

The Concept of Homology Is Basic to Determining Animal Relationships 11

Linnean and Hennigian Taxa Have Different Properties 12

Genealogical Histories Can Be Traced in Trees, Which Are Positional Structures 13

Morphological Entities within Metazoan Bodies, Such as Cells, Can Be Positioned in Trees 14

Trees Composed of Individual Organisms Can Be Incredibly Complicated 14

Trees Composed of Species Are Much Simpler 15

Trees Can Be Formed of Linnean Taxa above the Species Level 15

Molecular Information Can Position Morphologically Based Taxa in a Tree 15

Natural Biological Hierarchies Are Nested Structures of Functional Entities That Emerge When Complex Systems Are Organized 16

There Are Four Major Types of Hierarchical Structure 16

Hierarchies Help Sort Out Relations among Biological Features 20

Novel Phenomena Emerge at Successive Hierarchical Levels • The Effects of Levels upon One Another Are Quite Asymmetrical

Natural Hierarchies Are Formed by Trees 22

An Ecological Hierarchy of Biotic Entities Is Formed by the Tree of Life 22

Hierarchies of Genes Can Be Mapped onto the Somatic and Ecological Hierarchies 23

The Linnean Hierarchy Is Quasi-Natural 24

Trees and Hierarchies Have Very Distinct Properties 25

- Cladistics Is a Systematics Based on Trees 27**
Some Cladistic Terms Are Hypotheses as to the Evolutionary Status of Characters 27
In Cladistic Classifications, Branch Points May Define Sister Taxa That Are Holophyletic 29

Phyla Have Split Personalities 31

Molecular Branchings Can Define Clades, while Morphological Features Define Linnean Taxa 32

- Bodyplans Consist of Evolutionarily Disparate Features 33**
Bodyplans Are Polythetic 33
Important Bodyplan Features May Be Plesiomorphies or Synapomorphies, and May Be Homoplasies 33

Systematic Hierarchies and Trees: A Summary 37

2 Design Elements in the Bodyplans of Phyla 40

- Cells Are the Basic Building Blocks of Metazoan Bodies 40**
Cytoskeletons Provide the Framework for Cytoarchitectures 41
Metazoan Cells Have Descended from Protistans, Probably Choanoflagellate-Like 43

- Cells Are Integrated into Tissues by Protein Bindings or Matrices 45**
Extracellular Matrix Supports Metazoan Tissues 45
In Most Metazoan Tissues, Cells Are Connected or Anchored by Protein Molecules 45

- Metazoans Have Several Major Types of Tissues 47**
Most Tissues Are Epithelial or Connective 47
Muscle Tissue May Be either Epithelial or Connective 47
Nervous Tissues Are Not Organized either as Epithelia or as Connective Tissues 49
Multinucleate (Syncytial) Tissues Are Found in Many Disparate Phyla 49

Organs and Organ Systems Are Formed of Tissues 49

- Organisms Are Best Understood as Developmental Systems 50**
Cleavage and Cell Differentiation Are Linked in Most Metazoan Ontogenies 50
Gastrulation Gives Rise to Ectodermal and Endodermal Germ Layers 55
Middle Body Layers Range from Simple Sheets of Extracellular Matrix to Mesodermal Germ Layers 55
Pseudocoels and Hemocoels Are Body Cavities That Lie on the Site of the Blastocoel 59

Coeloms Are Body Cavities That Lie within Mesoderm 60

Some Coeloms Function as Hydrostatic Skeletons • Some Coeloms Are Adjuncts
to Organs

Larval Stages Commonly Possess Bodyplans of Their Own 62

Many Bodyplan Features Reflect Locomotory Techniques 64

In Soft-Bodied Forms, Locomotory Devices Range from Cilia to Limbs 64

*"Hard" Skeletons May Complement or Replace the Biomechanical Functions
of Fluid Skeletons* 65

Symmetry and Seriation Are the Principal Descriptors of Body Style 66

Symmetry Is Imparted by Repetition of Parts across Planes or along Radii 67

*Anteroposterior Regionation Involves Seriation, Segmentation,
and Tagmosis* 68

Evolutionary Changes in Body Size Occur throughout Metazoan
History 70

Area/Volume Ratios Are Sensitive to Most Size Changes 70

Life Is Different at High versus Low Reynolds Numbers 71

Morphological Complexity Is Not a Simple Topic 72

3 Development and Bodyplans 76

The Evolution of Developmental Systems Underpins the Evolution
of Bodyplans 76

The English Language and Genomes Both Have Combinatorial,
Hierarchical Structures 77

*In Narrative English the Immensity of Combinations Inherent in the Alphabet
Is Constrained within a Hierarchy* 77

Hierarchical Constraints Also Operate within Metazoan Genomes 79

The Metazoan Gene Is a Complex of Regulatory, Transcribed, and
Translated Parts 80

Transcribed Gene Regions Are Processed to Produce mRNA 80

Cis-Regulatory Elements Mediate Transcription 81

Regulatory Signals Are Produced by Trans-Regulatory Systems 83

Transcription Factors Bind to Enhancers 83

*Trans-Regulators Are Controlled by Signals That Ultimately Arise from Other
Regulatory Genes* 85

Genomic Complexity Is a Function of Gene Numbers and Interactions 86

Metazoan Genomes Display Surprising Patterns of Similarities and
Differences among Taxa 88

<i>Some Functional Classes of Genes Are Broadly Similar across Metazoan Phyla</i>	90
<i>Bodyplans Are Patterned by Sequential Expressions of High-Level Regulatory Genes</i>	91
<i>Anteroposterior Axis Specification and Patterning Genes Are Found throughout Eumetazoa</i>	92
<i>Dorsoventral Axis Specification and Patterning Genes Are Similar across Bilateria</i>	97
<i>Organogenesis Involves Positioning by Patterning Genes and Development via Gene Cascades Controlled by Selector Genes</i>	100
<i>Signaling Pathways, Like Individual Genes, Are Recruited for a Variety of Tasks</i>	103

Developmental Genomes May Evolve on Many, Semidecomposable Levels 103

<i>Evolution of Cis-Regulatory Elements Entails Effects That Differ from the Evolution of Transcribed Genes</i>	103
<i>Regulatory Variation May Be Maintained by Several Unique Mechanisms</i>	105
<i>Units of Selection in Developmental Evolution Include Semi-independent Modules</i>	107
<i>Bodyplan Evolution Commonly Uses Established Genetic Units of Selection for Novelties</i>	109
<i>Genes May Be Recruited or Captured • Cases of Heterochrony and Heterotopy Are Changes in the Time or Place of Gene Expression</i>	

Regulatory Gene Systems Organize Complexity 112

<i>The Developmental Genome Should Be Hierarchical</i>	112
<i>Networks That Organize the Products of a Tree into a Hierarchy Are Hypothesized to Be Scale-Free</i>	112
<i>Regulatory Genes Are Arbiters of Developmental Narratives</i>	114

4 Morphological and Molecular Phylogenies 115

Assumed Evolutionary Histories Affect Morphologically Based Phylogenetic Hypotheses 115

Many of the Classic Phylogenetic Hypotheses Involve Assumptions as to the Phylogenetic History of the Coelom 119

<i>Dichotomous Coelom Theories Postulate an Early Branching between Protostomes and Deuterostomes from a Common Ancestor</i>	119
<i>Enterocoel Theories Postulate That Enterocoely Is a Primitive Feature of Bilaterians</i>	120
<i>Schizocoel Theories Derive "the Coelom" from a Spiralian Acoelomate</i>	122
<i>Morphological Phylogenies Can Use Some Help</i>	123

Evolutionary Histories Affect Molecularly Based Estimates of the Timing, Branching Patterns, and Order of Origins of Phyla 123

The Dating of Deep Nodes by Molecular Clocks Is Problematic as Yet 123

Dating Nodes Does Not Date the Origin of Bodyplans 126

Genes That Are Phylogenetically Informative for Higher Taxa Must Evolve Slowly but Not Too Slowly 126

Variations in the Rate of Gene-Sequence Change among Taxa Can Produce False Molecular Phylogenies 127

Homologous Positions Must Be Aligned When Comparing Gene Sequences 130

Some Clades Are Characterized by a Natural Bias in Nucleotide Substitutions 131

Morphological and Molecular Homologies Are Decomposable 131

During Evolution, Morphological Hierarchies Are Dynamic Structures, and the Composition of Their Entities Is Somewhat Fluid 131

Molecular Homologies Do Not Necessarily Map on Morphological Homologies 131

There Is a Large Variety of Ways to Form Trees from Molecular Sequences 132

Distance Methods Estimate the Mean Number of Changes between Species 133

Parsimony Methods Find Trees That Minimize the Amount of Evolutionary Change Required to Produce Observed Sequences 134

Invariant Methods Concentrate on Reducing Long-Branch Attraction 135

Likelihood Methods Estimate Actual Change under a Given Evolutionary Model 135

Several Methods Help Evaluate the Quality of Support for Given Nodes 136

There Are Some Remedies for What Ails Molecular Trees 136

Although Molecular Phylogenies Produce Conflicting Topologies, They Have Also Produced a Growing Consensus on Major Alliances of Phyla 138

Early Studies Suggested Surprising Alliances of Phyla 138

Subsequent Work Has Tended to Support the Existence of Several Major Metazoan Alliances 141

Combined Morphological/Molecular Phylogenies of Phyla May Require Improved Assessments of Homologies to Be Successful 143

Stratigraphic Data Can Add Useful Information to Phylogenetic Hypotheses 146

The Alliances of Phyla Indicated by Molecular Methods Provide Evidence for Evaluating the Origin and Early History of Phyla 148

Prokaryotic Alliances Can Be Identified in a Very Conservative SSU rRNA Tree 148

The Conservative Tree May Be Modified by Other Criteria to Produce a More Liberal Hypothesis 149

Fossil Record 153

Stratigraphic Record Is Incomplete in a Spotty Way 153

Sedimentary Rocks Are Accumulated and Preserved Episodically 153

Sedimentary "Completeness" Varies with the Resolution That Is Desired 157

The Completeness of Sedimentary Sections Is Independent of Their Ages 159

Marine Fossil Record, while Incomplete, Yields Useful Samples of a Rather Consistent Fraction of the Fauna 160

Local Fossil Assemblages Are Largely Durably Skeletonized and Time-Averaged 160

Many Local Faunas Are Required in order to Estimate Global Diversity at Times of High Environmental Heterogeneity 162

Jumping Preservational Gaps Is Possible by Extrapolation between Rich Faunal Horizons 163

The Known Geologic Ranges of Taxa Are Sensitive to Their Fossil Abundances 164

There Are Ways of Coping with Incomplete Records 167

Taxonomic Completeness Increases at Higher Levels of the Taxonomic Hierarchy 167

Taxonomic Completeness Rises as Larger Bins Are Used to Increase Time-Averaging 167

Paleoecological and Biogeographic Completeness Increase at Higher Levels of the Ecological Hierarchy 168

Data from Coarser Units May Be Tested by Local Fine-Scale Studies 168

Neoproterozoic-Cambrian Fossil Record Provides the Only Direct Evidence of Early Metazoan Bodyplans 168

Satisfactory Definition and Dating of Late Neoproterozoic and Cambrian Rocks Have Been Accomplished Only Recently 169

Criteria for Defining the Neoproterozoic-Cambrian Boundary Have Varied over the Years • The Age of the Late Neoproterozoic-Early Cambrian Sequence Has Been Established Chiefly by Precision Dating of Zircon Crystals

Late Neoproterozoic and Early Cambrian Geographies Were Very Different from Today's 172

Knowledge of Late Neoproterozoic and Cambrian Faunas Has Greatly Increased in Recent Decades 174

Late Neoproterozoic Fossils Include Enigmatic Soft-Bodied Forms and Traces •
 Earliest Cambrian Faunal Traces Indicate Increases in Body Size and in Biological
 Activities • Numbers of Crown Phyla Appear during the Cambrian Explosion • The
 Middle Cambrian Contains Spectacular Faunas, but No Crown Phyla Appear for the
 First Time • Phyla That First Appear after the Explosion Are Soft-Bodied with One
 Exception (Bryozoa)

*If All Phyla Were Present by the Close of the Explosion, Their Records Agree
 Well with Expectations Based on Their Preservabilities* 186

*The Lack of Neoproterozoic Fossil Ancestors of Living Phyla Is Not Inconsistent
 with the Quality of the Fossil Record* 187

There Is a Vast Range of Hypotheses That Attempt to Explain the
 Cambrian Explosion 189

Perhaps There Was No Cambrian Explosion 191

The Explosion Was Due to Physical Changes in the Environment 191

The Explosion Was Due to Biological Changes in the Environment 193

The Explosion Reflects Intrinsic Evolutionary Change 194

In Sum, the Cambrian Fossils Imply an Explosion of Bodyplans, but the
 Underlying Causes Remain Uncertain 194

PART TWO *The Metazoan Phyla*

197

6 Prebilaterians and Earliest Crown Bilaterians 201

Sponges and Spongiomorphs 201

Bodyplan of Porifera 201

Cellularia • Symplasma

Development in Porifera 205

Cellularia • Symplasma

Fossil Record of Sponges and Spongiomorphs 208

Porifera • Archaeocyatha • Radiocyatha • Chancelloriidae

Poriferan Ancestry and Early Radiation of the Sponge Grade 211

Cnidarians and Cnidariomorphs 214

Bodyplan of Cnidaria 214

Development in Cnidaria 218

Early Fossil Cnidaria and Cnidariomorphs 219

The Vendobiont Hypothesis 225

Cnidarian Relationships and Early Radiation of Cnidariomorphs 226

Ctenophora 228

Bodyplan of Ctenophora 228

Development in Ctenophora 228

Fossil Record of Ctenophora 230

Ctenophoran Relationships 231

Placozoa 232

Myxozoa 233

Diversification of Prebilaterian Metazoa 234

Acoelomorpha: Earliest Crown Bilaterians? 236

Bodyplan of Acoelomorpha 237

Development in Acoelomorpha 239

Fossil Record of Acoelomorpha 240

Acoelomorphs and the Early Bilateria 240

7 Protostomes: The Ecdysozoa 241

Priapulida 241

Bodyplan of Priapulida 241

Development in Priapulida 243

Fossil Record of Priapulida 243

Kinorhyncha 244

Bodyplan of Kinorhyncha 244

Development in Kinorhyncha 246

Fossil Record of Kinorhyncha 246

Loricifera 246

Bodyplan of Loricifera 246

Development in Loricifera 248

Fossil Record of Loricifera 248

Nematomorpha 248

Bodyplan of Nematomorpha 248

Development in Nematomorpha 249

Fossil Record of Nematomorpha 250

Nematoda 250

Bodyplan of Nematoda 250

Development in Nematoda 252

Fossil Record of Nematoda 255

Paleoscolecidae 256

Relationships of Paracoelomate Ecdysozoans 257

Onychophora 257

- Bodyplan of Onychophora* 258
- Development in Onychophora* 259
- Onychophora and Fossil Lobopods* 259
 - Aysheaia, Luolishania, and Xenusion* • Armored Lobopods • Later Forms
- Relationships among Living and Fossil Onychophorans* 262

Tardigrada 262

- Bodyplan of Tardigrada* 263
- Development in Tardigrada* 264
- Fossil Record of Tardigrada* 264

Arthropoda 264

- Bodyplan of Arthropoda* 264
 - Major Clades • Pentastomids
- Development in Arthropoda* 271
- Early Fossil Record of Arthropoda* 275
- Early Fossil Relatives (or Perhaps Basal Stem Groups) of Arthropoda* 281

Some Branch Points within the Ecdysozoa 283

- Nodes 1, 2, and 3* 283
- Nodes 4 and 5* 284
- Onychophora + Tardigrada + Arthropoda Clade* 284
 - Onychophora • Tardigrada • Arthropoda
- Ecdysozoan Cleavages* 285

Early History of the Lobopodian and Arthropodan Clades 286

8 Protostomes: Lophotrochozoa 1: Eutrochozoans 288

Platyhelminthes: Rhabditophora and Catenulida 288

- Bodyplan of Platyhelminthes* 290
 - Free-Living Rhabditophora • Catenulida • *Xenoturbella* • Some Flatworm
 - Bodyplan Variations
- Development in Marine Rhabditophora* 293
- Fossil Record of Flatworms* 294
- Flatworm Relationships* 294

Mollusca and Mollusklike Forms 295

- Bodyplan of Mollusca* 295
- Development in Mollusca* 301
- Early Fossil Record of Mollusca* 302
- Early Fossil Record of Mollusklike Forms* 308
 - Acaenoplax* • Probivalvia or Stenothecoida • Hyolitha • *Kimberella*
- Molluscan Relationships* 310

Annelida 312

Bodyplan of Annelida 314

Development in Annelida 319

Pogonophora 320

Bodyplan of Pogonophora • Development in Pogonophora

Echiura 322

Bodyplan of Echiura • Development in Echiura

Fossil Record of Annelida 324

Pogonophora • Echiura

Annelid Ancestry 326

Sipuncula 326

Bodyplan of Sipuncula 326

Development in Sipuncula 328

Fossil Record of Sipuncula 328

Sipunculan Relationships 328

Nemertea 328

Bodyplan of Nemertea 329

Development in Nemertea 330

Fossil Record of Nemertea 331

Nemertean Relationships 331

Mesozoans: Rhombozoa and Orthonectida 331

Bodyplans of Mesozoans 332

Development in Mesozoans 332

Mesozoan Relationships 333

Fossil Groups That May Be Eutrochozoans 333

Coeloscleritophora 333

Turrilepadida 335

Fascivermis 336

Other Groups of Problematica 336

Possible Branch Points within Eutrochozoa 337

9 Protostomes: Lophotrochozoa 2: Lophophorates 339

Bryozoa 339

Bodyplan of Bryozoa 339

Development in Bryozoa 342

Ontogeny • Astogeny (Colony Development)

Fossil Record of Bryozoa 343

Bryozoan Relationships 343

Phoronida 345*Bodyplan of Phoronida 345**Development in Phoronida 346**Fossil Record of Phoronida 348**Phoronid Relationships 348***Brachiopoda 348***Bodyplan of Brachiopoda 350**Development in Brachiopoda 353**Fossil Record of Brachiopoda 354**Extinct Brachiopod-like Forms 354**Brachiopod Relationships 355***Lophophorate Relationships 356****10 Protostomes: Paracoelomates 360****Gastrotricha 361***Bodyplan of Gastrotricha 361**Development in Gastrotricha 361**Fossil Record of Gastrotricha 363**Gastrotrich Relationships 363***Rotifera 363***Bodyplan of Rotifera 363**Development in Rotifera 364**Fossil Record of Rotifera 365**Rotiferan Relationships 365***Acanthocephala 365***Bodyplan of Acanthocephala 365**Development in Acanthocephala 366**Fossil Record of Acanthocephala 367**Acanthocephalan Relationships 367***Entoprocta 368***Bodyplan of Entoprocta 368**Development in Entoprocta 369**Fossil Record of Entoprocta 370**Entoproctan Relationships 370***Cycliophora 370***Bodyplan of Cycliophora 371**Development in Cycliophora 372**Fossil Record of Cycliophora 372**Cycliophoran Relationships 372*

Gnathostomulida 372

- Bodyplan of Gnathostomulida* 372
- Development in Gnathostomulida* 373
- Fossil Record of Gnathostomulida* 373
- Gnathostomulid Relationships* 373

Chaetognatha 374

- Bodyplan of Chaetognatha* 374
- Development in Chaetognatha* 375
- Fossil Record of Chaetognatha* 376
- Chaetognath Relationships* 376

Phylogenetic Schemes for Paracoelomates 377

- Major Schemes for Vermiform Paracoelomates* 377
- The Fossil Record and Paracoelomate Histories* 378

II Deuterostomes 381

Hemichordata 383

- Bodyplan of Enteropneust Hemichordata* 383
- Bodyplan of Pterobranch Hemichordata* 385
- Development in Hemichordata* 387
- Fossil Record of Hemichordata* 388
 - Enteropneusta • Pterobranchia • Graptolithina
- Hemichordate Relationships and Ancestry* 390

Echinodermata 391

- Bodyplan of Echinodermata* 391
- Development in Echinodermata* 394
- Fossil Record of Echinodermata* 397
 - Crinozoa • Blastozoa • Echinozoa • Homalozoa • The Echinoderm Skeleton
- Echinoderm Ancestry* 404

Vetulicolia 406

Invertebrate Chordata 406

- Urochordata* 406
 - Bodyplan of Ascidiacea • Development in Ascidiacea • Bodyplan of Appendicularia (Larvacea) • Development in Appendicularia • Fossil Record of Urochordata • Urochordate Ancestry
- Cephalochordata* 413
 - Bodyplan of Cephalochordata • Development in Cephalochordata • Fossil Record of Cephalochordata
- Other Possible Invertebrate Chordates* 417

- Early Vertebrata 418
 Earliest Agnathans 418
 Euconodonta 418
 Paraconodonta 421

- Chordate Ancestry 421
 Older Scenarios 421
 Revised Scenarios 422

PART THREE *Evolution of the Phyla*

425

12 Phanerozoic History of Phyla 429

Diversification Patterns of Higher Taxa with Mineralized Skeletons
 Can Be Evaluated by Richnesses and Disparities 431

Taxonomic Disparity Commonly Reached High Levels Early in Clade

History 431

Bryozoa Radiated at the Ordinal Level while at Low Diversity • Brachiopoda Also
 Radiated at the Ordinal Level while at Low Diversity • Mollusca Produced
 Disparate Stem Groups in the Early Cambrian • Echinodermata Diversified into
 Disparate Clades from Early Cambrian to Middle Ordovician Time • Other Durably
 Skeletonized Phyla Show High Early Disparity, and the Records of Soft-Bodied
 Forms Are Not Inconsistent with Such a Pattern

*Morphometric Disparity Has Been Evaluated Only within Phylum Subclades,
 Which Sometimes Reach High Levels Early in Clade History* 438

Within Blastozoa and Crinoidea (Echinodermata) High Morphological Disparity
 Is Achieved Early • Among Mollusca, Gastropoda Shows Larger Early Morphological
 Disparities while Rostroconcha Shows a Complicated Pattern • Trilobita Are Most
 Disparate Well after Their First Appearance

Within Phyla, Disparity and Diversity Seem to Be Independent 443

Macroevolutionary Dynamics of Phyla Run the Gamut from Stability
 to Volatility 445

Clade Dynamics Reflect Speciation and Extinction Rates 445

*Macroevolutionary "Competition" Arises from Differential Speciation and
 Extinction Rates* 447

Linnean Taxa May Form Macroevolutionarily Dynamic Units 448

Sorting Strategies Arise from Selection among Individuals 449

Clade Histories of Invertebrate Taxa with Mineralized Skeletons Reflect
 Turnover Dynamics 452

*There Are Hints That the Origin of Marine Clades Is Favored in Shallow
 Tropical Waters* 452

Turnover Rates Influence Clade “Shape” over Time 453

The Early History of Phyla Is Consistent with the Evolutionary Patterns Shown Following the Cambrian 458

Is the Number of Phyla Related to the Gross Heterogeneity of the Marine Environment? 460

The Late Neoproterozoic and Early Cambrian Pattern of Appearances Is Consistent with Patterns Found throughout the Phanerozoic 463

13 Metazoan Evolution during the Prelude to the Cambrian Explosion 465

Metazoan Multicellularity Evolved from Protistan Pluricellularity 466

Protistans Set the Stage 466

A Novel Bodyplan Involving Differentiated Cell Types Founded the Kingdom Metazoa 467

The Complexity of Metazoan Bodies Led to the Emergence of a Hierarchical Somatic Organization and to Hierarchical, Scale-Free Networks within the Developmental Genome 469

Diploblastic Somatic Architecture Evolved from Sponges 471

Diploblastic Bodyplans Employ Epithelia 471

The Developmental Genomes of Prebilaterians Are Foreshadowed in Their Protistan Ancestors 473

The Nature of Early Bilateria Is Widely Debated 475

The Prebilaterian/Bilaterian Gap Is Wide 475

The Earliest Bilaterians May Descend from Stem Diploblastic Larvae 476

The Trochaea Hypothesis Proposes Evolution in the Plankton • The Set-Aside

Hypothesis Proposes Evolution via Deferred Complexity • The Colonial

Hypothesis Proposes Evolution via Rounds of Individuation • The

Planuloid Hypothesis Proposes Benthic Evolution with Complexity Increases

within the Somatic Hierarchy

A Benthic Hypothesis Can Explain Both Fossil and Molecular Data and Is Not Incompatible with Developmental Patterns 484

Molecular Norms of Metazoan Development Were Established in Prebilaterian Genomes 484

The Early Bilaterians Presumably Radiated during the Prelude to Produce a Diverse Paracoelomate Fauna 485

Cleavages and Larval Modes Are Related in Extant Bilaterians, and Suggest Models for the Fauna of the Prelude 487

Larval Modes and Therefore Cleavage Patterns Are Related to Environmental Conditions 488

Cleavage Patterns among Living Clades May Reflect the History of Their Larval Modes 490

Ectoderm, Endoderm, and Endomesoderm Are Probably Homologous throughout the Eumetazoa 492

Crown Paracoelomate Bodyplans Largely Represent a Radiation of Small-Bodied Protostomes 493

Metazoan Complexity Increased before the Cambrian Explosion, Perhaps Chiefly during the Early Cambrian 493

14 Metazoan Evolution during the Cambrian Explosion and Its Aftermath 497

Independent Trends in Body-Size Increases Produced the Major Bilaterian Alliances 497

The Degree of Disparity among Neoproterozoic Paracoelomates Is Entirely Conjectural 497

Cambrian Selection for Body-Size Increases Involved Regulation of Cell-Division Cycles 497

The Homology of Body Cavities across Bilateria Is Unlikely 498

Primary Body Cavities—Pseudocoels and Hemocoels—Have Been Lost in Some Lineages but Are Main Body Spaces in Others 498

Secondary Body Cavities—Coeloms—Are Highly Functional and Are Not Likely to Be Homologous across Bilateria 499

Systems Associated with Body Cavities, Such as Blood Vascular and Nephridial Systems, May Be Homoplastic 500

Body-Size Increases Are Consistent with the Early Cambrian Evolution of Planktotrophy and Divergences in Early Development 503

There Are Similarities in the Gross Morphological Adaptations of Some Phyla in the Separate Alliances 505

Deuterostomes Radiated in Two Major Clades, One of Which Evolved a Notochord, and the Rest Is History 506

Adaptive Trends within Ecdysozoa Implicate the Molting Habit as Providing Both Major Opportunities and Constraints 508

Lophotrochozoan Phylogeny Is Problematic, Suggesting a Rapid Radiation from the Crown Ancestor 510

The Remaining Protostomes Are Still a Troublesome Group 513

The Cambrian Explosion Produced Widespread Homoplasy:
A Summary 513

Much Evolution of the Developmental Genome Occurred in the Service
of Bodyplan Originations: A Summary 514

Why Are Problems of Early Metazoan Evolution So Hard? 516

If Only It Were Just the Data 516

The Incredible Richness of Choice 517

Closing Thoughts 518

Appendix: The Geologic Time Scale 521

Glossary 525

References 533

Index 607