Contents

Preface xxiii

PART ONE Evidence of the Origins of Metazoan Phyla

Ι

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

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

Developmental Genomes May Evolve on Many, Semidecomposable Levels 103

- Evolution of Cis-Regulatory Elements Entails Effects That Differ from the Evolution of Transcribed Genes 103
- Regulatory Variation May Be Maintained by Several Unique Mechanisms 105 Units of Selection in Developmental Evolution Include Semi-independent Modules 107
- Bodyplan Evolution Commonly Uses Established Genetic Units of Selection for Novelties 109

Genes May Be Recruited or Captured • Cases of Heterochrony and Heterotopy Are Changes in the Time or Place of Gene Expression

Regulatory Gene Systems Organize Complexity 112 The Developmental Genome Should Be Hierarchical 112 Networks That Organize the Products of a Tree into a Hierarchy Are Hypothesized to Be Scale-Free 112 Regulatory Genes Are Arbiters of Developmental Narratives 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

- Dichotomous Coelom Theories Postulate an Early Branching between Protostomes and Deuterostomes from a Common Ancestor 119
- Enterocoel Theories Postulate That Enterocoely Is a Primitive Feature of Bilaterians 120

Schizocoel Theories Derive "the Coelom" from a Spiralian Acoelomate 122 Morphological Phylogenies Can Use Some Help 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 Bilaterian 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

5 The Fossil Record 153

The 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

The 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

The 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

xvi CONTENTS

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

CONTENTS XVII

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

xviii CONTENTS

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

11 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

Fossil Record of Cycliophen

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

xxii CONTENTS

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