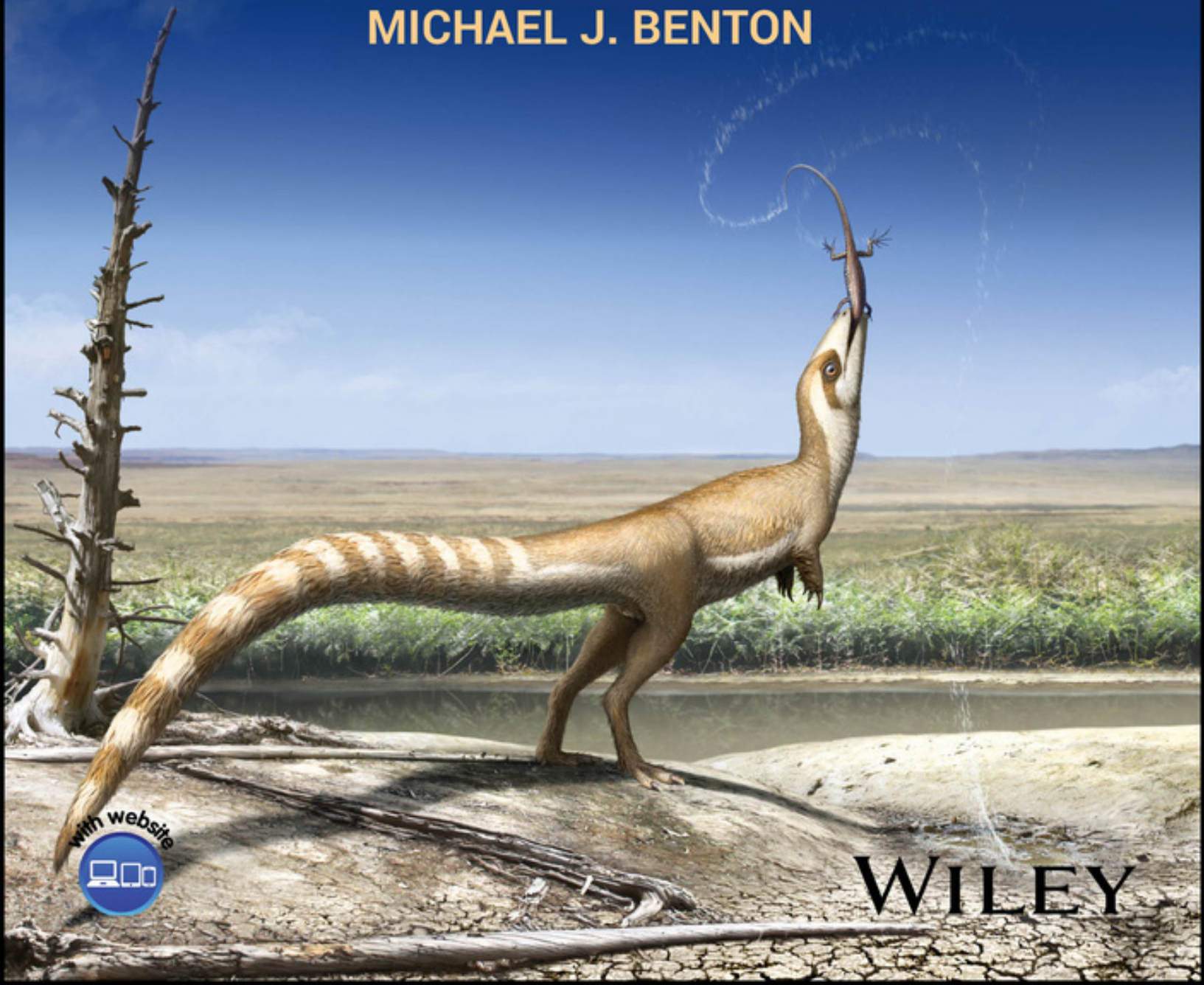


FIFTH EDITION

VERTEBRATE PALAEOONTOLOGY

MICHAEL J. BENTON



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Vertebrate Palaeontology

Fifth Edition

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Dedicated to Mary, for her good-humoured acceptance of my six months of absent mindedness while I revised this book.

Contents

	List of Boxes	<i>xvii</i>
	Preface	<i>xxi</i>
	About the Companion Website	<i>xxv</i>
1	Vertebrates Originate	1
	Introduction	1
1.1	Sea Squirts and the Lancelet	2
1.1.1	Cephalochordata: Amphioxus	2
1.1.2	Urochordata: Sea Squirts	2
1.2	Ambulacraria: Echinoderms and Hemichordates	4
1.2.1	Echinodermata: Sea Urchins and Starfish	4
1.2.2	Hemichordata: Pterobranchs and Acorn Worms	5
1.2.3	Ambulacrarian Origins	6
1.3	Deuterostome Relationships	6
1.3.1	Embryology and the Position of the Anus	8
1.3.2	Animal Phylogenomics	9
1.4	Chordate Origins	9
1.4.1	Diverse Early Chordates	10
1.4.2	Vetulicolia	12
1.4.3	<i>Pikaia</i>	13
1.4.4	Yunnanozoa	13
1.5	Vertebrate Origins: Worm or Bag?	15
1.5.1	Tadpole Origins	17
1.5.2	Vertebrates and the Neural Crest	17
1.5.3	The Vertebrate Ancestor	19
1.6	Further Reading	20
	Questions for Future Research	20
	References	21
2	How to Study Fossil Vertebrates	25
	Introduction	25
2.1	Digging Up Bones	25
2.1.1	Collecting Fossil Vertebrates	25
2.1.2	Preparation and Conservation of Bones	28
2.1.3	3D Imaging	28
2.1.4	Display and Study	29
2.2	Publication and Professionalism	32
2.2.1	The Scientific Literature	32
2.2.2	How to Write a Scientific Paper	33

2.2.3	The Journal Review and Publication Process	36
2.2.4	Careers in Vertebrate Palaeontology	37
2.3	Geology and Fossil Vertebrates	37
2.3.1	Taphonomy	39
2.3.2	Palaeogeography	42
2.3.3	Palaeoclimate	44
2.4	Biology and Fossil Vertebrates	46
2.4.1	Functional Morphology	46
2.4.2	Computational Methods in Functional Morphology	48
2.4.3	Palaeoecology	51
2.5	Discovering Phylogeny	53
2.5.1	Cladistic Analysis of Morphological Characters	53
2.5.2	Molecular Phylogenetics	55
2.6	Macroevolution	56
2.7	Further Reading	59
	References	59
3	Early Palaeozoic Fishes	63
	Introduction	63
3.1	Cambrian Vertebrates	63
3.2	Vertebrate Hard Tissues	65
3.2.1	Bone	65
3.2.2	Origins of Teeth: Inside Out or Outside In?	67
3.3	The Jawless Fishes	67
3.3.1	Cyclostomata: The Living Jawless Fishes	69
3.3.2	Conodonts	71
3.3.3	Ordovician Jawless Fishes	73
3.3.4	Heterostraci	74
3.3.5	Anaspida and Thelodonti	75
3.3.6	Osteostraci and Relatives	76
3.4	Origin of Jaws	80
3.4.1	Jaws	80
3.4.2	Jaw Attachments and Gnathostome Relationships	82
3.5	Placoderms: Armour-Plated Monsters	82
3.5.1	Arthrodira	83
3.5.2	Placoderm Palaeobiology	86
3.5.3	Diverse Placoderms	86
3.6	Pan-Chondrichthyes: Sharks, Rays, Acanthodians	90
3.7	Early Fish Biogeography and Environments	92
3.7.1	Siluro-Devonian Faunal Provinces	92
3.7.2	Siluro-Devonian Environments	93
3.8	Osteichthyes: The Bony Fishes	94
3.8.1	Devonian Actinopterygians	96
3.8.2	Actinistia: The Coelacanth	98
3.8.3	Dipnoi: The Lungfishes	101
3.8.4	Early Sarcopterygians: Origins of Tetrapodomorpha	103
3.9	Early Fish Evolution and Mass Extinction	106
3.9.1	Diversification of Early Vertebrates	106
3.9.2	The Late Devonian Mass Extinctions	106
3.10	Further Reading	107
	Questions for Future Research	108
	References	108

4 The First Tetrapods 115

- Introduction 115
- 4.1 Problems of Life on Land 115
 - 4.1.1 Support 116
 - 4.1.2 Locomotion 116
 - 4.1.3 Feeding and Respiration 118
 - 4.1.4 Sensory Systems and Water Balance 119
 - 4.1.5 Reproduction 120
- 4.2 Devonian Tetrapods 120
 - 4.2.1 Anatomy 122
 - 4.2.2 How Many Fingers and Toes? 126
 - 4.2.3 Modes of Life of the First Tetrapods 127
- 4.3 The Carboniferous World 128
 - 4.3.1 Romer's Gap 128
 - 4.3.2 The Carboniferous Scene 129
- 4.4 Diversity of Carboniferous Tetrapods 129
 - 4.4.1 Early Carboniferous Tetrapods 129
 - 4.4.2 Temnospondyli 132
 - 4.4.3 Early Reptiliomorpha: Embolomeri and Gephyrostegidae 133
 - 4.4.4 Lepspondyli 134
 - 4.4.5 Vertebral Evolution 138
 - 4.4.6 The Carboniferous Rainforest Collapse 139
- 4.5 Temnospondyls and Reptiliomorphs After the Carboniferous 139
 - 4.5.1 Temnospondyli: Permian to Cretaceous History 139
 - 4.5.2 Seymouriamorpha 143
 - 4.5.3 Diadectomorpha 144
- 4.6 Evolution of the Modern Amphibians 144
 - 4.6.1 Albanerpetontidae 144
 - 4.6.2 Anura (Salientia) 146
 - 4.6.3 Urodela (Caudata) 147
 - 4.6.4 Gymnophiona (Apoda) 149
 - 4.6.5 Origin of the Modern Amphibians 149
- 4.7 Further Reading 150
 - Questions for Future Research 150
 - References 150

5 Evolution of Early Amniotes 157

- Introduction 157
- 5.1 *Hylonomus* and *Paleothyris* – Biology of the First Amniotes 157
 - 5.1.1 The Amniote Skull 157
 - 5.1.2 The Amniote Skeleton 159
 - 5.1.3 Palaeobiology of the First Amniotes 160
- 5.2 Amniote Adaptations for Terrestrial Life 160
 - 5.2.1 Controlling Water Loss 163
 - 5.2.2 Amniote Adaptations for Walking, Feeding, and Breathing on Land 163
 - 5.2.3 Reproduction on Land 164
 - 5.2.4 Temporal Fenestrae 167
- 5.3 The Permian World 167
- 5.4 The Parareptiles 169
 - 5.4.1 Mesosauridae 169
 - 5.4.2 Millerettidae 170
 - 5.4.3 Lanthanosuchoidea 170

- 5.4.4 Bolosauridae 170
- 5.4.5 Procolophonidae 171
- 5.4.6 Pareiasauromorpha: Nycteroleters and Pareiasaurs 171
- 5.5 The Eureptiles 174
 - 5.5.1 Captorhinidae 174
 - 5.5.2 *Paleothyris* and *Hylonomus* 175
 - 5.5.3 Early Diverging Diapsids 175
 - 5.5.4 Permian Diapsids 175
- 5.6 Early Synapsid Evolution 176
 - 5.6.1 Carboniferous and Early Permian Synapsids 178
 - 5.6.2 The Sail-Backed Synapsids 179
 - 5.6.3 Biarmosuchia: The First Therapsids 180
 - 5.6.4 Dinocephalia 180
 - 5.6.5 Anomodontia 182
 - 5.6.6 Gorgonopsia 186
 - 5.6.7 Therocephalia 187
 - 5.6.8 Cynodontia 188
- 5.7 The Permian-Triassic Mass Extinction 188
- 5.8 Further Reading 192
 - Questions for Future Research 192
 - References 193

6 The Triassic Revolution 197

- Introduction 197
- 6.1 The Triassic World and the Recovery of Life 197
 - 6.1.1 The Triassic World and Recovering Environments 198
 - 6.1.2 Early Triassic Recovery of Life 198
 - 6.1.3 The Ecology of Recovery 200
 - 6.1.4 Bottlenecks and Explosions 201
- 6.2 Triassic Marine Reptiles 202
 - 6.2.1 Thalattosauria 202
 - 6.2.2 Ichthyosauromorpha 202
 - 6.2.3 Saurosphargidae 206
 - 6.2.4 Placodontia 207
 - 6.2.5 Eosauropterygia: Pachypleurosauria and Nothosauria 207
 - 6.2.6 Diapsid Diversification in the Sea and on Land 209
- 6.3 Evolution of the Archosauromorphs 211
 - 6.3.1 Diverse Archosauromorphs 211
 - 6.3.2 Early Archosauriforms 212
 - 6.3.3 Pseudosuchia: Middle and Late Triassic Archosaur Diversity 215
 - 6.3.4 Crocodylomorpha: Origin of the Crocodylians 219
- 6.4 Origin of the Dinosaurs 220
 - 6.4.1 Avemetatarsalia: The First Forms 220
 - 6.4.2 Dinosauromorpha: Establishing Key Features of Dinosaurs 220
 - 6.4.3 Pterosauromorpha: Origins of the Flying Reptiles 223
 - 6.4.4 The First Dinosaurs 224
- 6.5 Amniote Evolution in the Triassic 224
 - 6.5.1 The Triassic Revolution 224
 - 6.5.2 Carnian Pluvial Episode 229
 - 6.5.3 Models for Dinosaurian Origins 232
 - 6.5.4 The End-Triassic Mass Extinction 235

6.6	Further Reading	235
	Questions for Future Research	235
	References	236
7	Evolution of Fishes After the Devonian	243
	Introduction	243
7.1	The Early Chimaeras and Sharks	243
7.1.1	Symmeriiformes	244
7.1.2	Eugeneodontiformes and Petalodontiformes	244
7.1.3	Holocephali and Extinct Stem Groups	244
7.1.4	Early Diverging Elasmobranchs	247
7.2	Post-Palaeozoic Chondrichthyan Radiation	251
7.2.1	Neoselachii: The Modern Sharks	251
7.2.2	Neoselachian Diversity	251
7.2.3	Changes in Hunting Style and the Neoselachian Radiation	255
7.3	The Early Bony Fishes	255
7.3.1	The Devonian Actinopterygians	257
7.3.2	Cladistians, Chondrosteans, and Relatives	257
7.3.3	The Neopterygian Explosion	261
7.3.4	Jaws and Feeding in Bony Fishes	267
7.4	Radiation of the Teleosts	267
7.4.1	Teleost Outgroups and Early Teleosts	267
7.4.2	Eloposteoglossocephala: Eels and Relatives	270
7.4.3	Otocephala: Herrings and Carp	271
7.4.4	Euteleostei: Salmon, Pike, and Derived Teleosts	272
7.4.5	Acanthomorpha	273
7.5	Post-Devonian Evolution of Fishes	276
7.6	Further Reading	279
	Questions for Future Research	279
	References	280
8	Dinosaurs	287
	Introduction	287
8.1	Biology of <i>Plateosaurus</i>	287
8.2	The Jurassic and Cretaceous World	289
8.3	Saurischians and Theropod Diversity	290
8.3.1	Dinosaur Hips and Hindlimbs	290
8.3.2	Early Diverging Theropods	291
8.3.3	Tetanurae	295
8.3.4	Coelurosauria	298
8.3.5	Maniraptora	301
8.4	The Sauropodomorph Dinosaurs	303
8.4.1	Early Branching Sauropodomorpha	303
8.4.2	Neosauropoda	305
8.5	The Diversity of Ornithischian Dinosaurs	309
8.5.1	The First Ornithischian	309
8.5.2	Thyreophora	309
8.5.3	Stegosauria: The Plated Dinosaurs	310
8.5.4	Ankylosauria: Armour-Covered Dinosaurs	311
8.5.5	Early Branching Neornithischia	312
8.5.6	Ornithopoda	315

- 8.5.7 Hadrosauroidea: The Duckbills 317
- 8.5.8 Pachycephalosauria: The Bone-Heads 322
- 8.5.9 Ceratopsia: The Horn-Faced Dinosaurs 323
- 8.6 Were the Dinosaurs Warm-Blooded or Not? 326
 - 8.6.1 The Evidence 326
 - 8.6.1.1 Feathers 326
 - 8.6.1.2 Isotopes 326
 - 8.6.1.3 Bone Histology 327
 - 8.6.1.4 Biomolecules 329
 - 8.6.1.5 Locomotory Mechanics 329
 - 8.6.2 Endothermy and Gigantothermy 330
 - 8.6.3 On Being a Giant 331
- 8.7 Further Reading 333
 - Questions for Future Research 334
 - References 334

- 9 The Mesozoic Reptiles 343**
 - Introduction 343
 - 9.1 Testudinata: The Turtles 343
 - 9.1.1 Turtle Anatomy 343
 - 9.1.2 Stem Turtles and Turtle Origins 346
 - 9.1.3 Meiolaniformes and Paracryptodira 349
 - 9.1.4 Testudines: The Modern Turtle Clade 350
 - 9.2 Crocodylomorpha 353
 - 9.2.1 Crocodylian Characteristics 353
 - 9.2.2 The First Crocodylomorphs 354
 - 9.2.3 Jurassic–Cretaceous Mesoeucrocodylia 355
 - 9.2.4 Neosuchia: Modern Crocodylians 358
 - 9.3 Pterosauria 359
 - 9.3.1 Pterosaur Anatomy and Ecology 360
 - 9.3.2 Giant Late Cretaceous Pterosaurs 361
 - 9.3.3 Pterosaur Walking 363
 - 9.3.4 Pterosaur Flight 364
 - 9.4 The Great Sea Dragons 367
 - 9.4.1 Ichthyopterygia 367
 - 9.4.2 Plesiosauria 370
 - 9.4.3 Ecomorphology of the Mesozoic Marine Reptiles 372
 - 9.5 Lepidosauria: Lizards and Snakes 374
 - 9.5.1 Rhynchocephalia: Reptilian ‘Living Fossils’ 374
 - 9.5.2 Squamata: The Lizards and Snakes 375
 - 9.5.3 Pansquamata 377
 - 9.5.4 Squamata 377
 - 9.5.5 Serpentes: The Snakes 382
 - 9.6 The End-Cretaceous Mass Extinction 383
 - 9.6.1 What Died Out? 383
 - 9.6.2 The Last Day of the Cretaceous 383
 - 9.6.3 A Whimper or a Bang? 385
 - 9.6.4 Ecological Upheaval in the Last Days of the Dinosaurs 388
 - 9.7 Further Reading 390
 - Questions for Future Research 390
 - References 390

10	The Birds	401
	Introduction	401
10.1	The Origin of Birds	401
10.1.1	Paraves	401
10.1.2	Feathers	405
10.1.3	<i>Archaeopteryx</i> Specimens and Preservation	407
10.1.4	Anatomy of <i>Archaeopteryx</i>	410
10.1.5	Paravian Relationships	411
10.2	The Origin of Bird Flight	412
10.2.1	Avian Endothermy	412
10.2.2	The Flight Apparatus of Modern Birds	413
10.2.3	Flight Mechanics and Modes in Birds	415
10.2.4	Flight Capabilities of Paravians	415
10.2.5	Trees Down or Ground Up?	417
10.3	Cretaceous Birds, With and Without Teeth	418
10.3.1	Tails and Pygostyles of Early Cretaceous Birds	418
10.3.2	Confuciusornithiformes: Toothless Birds from China	422
10.3.3	Enantiornithes: Most Diverse Cretaceous Bird Clade	423
10.3.4	Early Ornithuromorphs	426
10.3.5	Ichthyornithiformes: Toothed Fishers	427
10.3.6	Hesperornithiformes: Flightless Divers	428
10.4	The Radiation of Modern Birds: Explosion or Long Fuse?	429
10.4.1	Cretaceous Aves (Neornithes)	429
10.4.2	Molecular Dates	431
10.4.3	Birds and the End-Cretaceous Mass Extinction	432
10.5	Flightless Birds: Palaeognathae	432
10.6	Neognathae	435
10.6.1	Neognath Characters and Embryology	435
10.6.2	Neognath Phylogeny	435
10.6.3	Galloanserae: Ducks and Fowl	437
10.6.4	Columbea: Flamingos, Grebes, Doves, and Sandgrouse	438
10.6.5	Otidiae: Hummingbirds, Swifts, Cuckoos, Bustards, and Turacos	439
10.6.6	Gruae: Hoatzin, Rails, and Shorebirds	440
10.6.7	Phaethoquornithes: The Waterbird Clade	440
10.6.8	Afroaves: Landbirds with African Origins	444
10.6.9	Australaves: Landbirds with Australasian Origins	444
10.7	The Three-Phase Diversification of Birds	447
10.8	Further Reading	448
	Questions for Future Research	448
	References	449
11	Mammals: Origins and Southern Hemisphere Evolution	459
	Introduction	459
11.1	Cynodonts and the Acquisition of Mammaliaform Characters	459
11.1.1	The First Cynodonts	460
11.1.2	Cynognathia: Herbivorous Cynodonts and Others	463
11.1.3	Probainognathia	465
11.1.4	Cynodonts: From Reptiles to Mammals	465
11.1.5	Tritylodonts, Tritheledonts, and Brasilodonts	470
11.1.6	Cynodont Macroevolution	472

11.2	The First Mammaliaforms	472
11.2.1	The First Mammaliaforms	472
11.2.2	Morganucodont Anatomy	472
11.2.3	Morganucodont Biology	474
11.3	The Mesozoic Mammaliaforms	475
11.3.1	<i>Hadrocodium</i> and Docodonta	478
11.3.2	The Tribosphenic Molar	479
11.3.3	Australosphenida: Monotremes and Relatives	480
11.3.4	Early Diverging Theriimorpha	483
11.3.5	Allotheria and Haramiyida: Long-lived Extinct Clades	484
11.3.6	Multituberculates	485
11.3.7	Cladotheria: Cretaceous Stem Therians	487
11.3.8	Metatheria: Cretaceous Stem Marsupials	488
11.3.9	Eutheria: Jurassic and Cretaceous Placentals	489
11.3.10	Mammals and the End-Cretaceous Mass Extinction	492
11.4	Marsupials Down Under	492
11.4.1	Geography and Marsupial Migrations	493
11.4.2	The Australian Marsupials	494
11.5	South American Mammals – A World Apart	497
11.5.1	The Mesozoic Mammals of South America	497
11.5.2	South American Marsupials	497
11.5.3	Xenarthra: Armadillos, Sloths, and Anteaters	500
11.5.4	South American Native Ungulates	501
11.5.5	South American Waifs	505
11.5.6	The Great American Biotic Interchange	505
11.6	Afrotheria and the Break-up of Gondwana	506
11.6.1	Aardvarks, Tenrecs and Elephant Shrews	506
11.6.2	Hyracoidea and Sirenia: Hyraxes and Sea Cows	507
11.6.3	Proboscidea: Elephants and Relatives	509
11.7	Further Reading	512
	Questions for Future Research	513
	References	513
12	Mammals of the Northern Hemisphere	525
	Introduction	525
12.1	Evolution of Modern Mammals	525
12.1.1	The Evolution Revolution	525
12.1.2	Dating the Diversifications	527
12.2	Boreoeutherian Beginnings: The Palaeocene in the Northern Hemisphere	529
12.2.1	Small Palaeocene Mammals	529
12.2.2	Early Rooters and Browsers	532
12.2.3	Palaeocene Flesh-eaters	533
12.2.4	The Palaeocene Placental Explosion	534
12.2.5	Mammal Evolution: Internal or External Drivers?	536
12.3	Early Diverging Laurasiatherians: Eulipotyphla	537
12.4	Scrotifera: Bats and Relatives	540
12.5	Cetartiodactyla: Cattle, Pigs and Whales	540
12.5.1	Artiodactyla: Cattle, Deer, and Pigs	541
12.5.2	Tylopoda: Camels and Relatives	543
12.5.3	Suina: Pigs and Peccaries	543
12.5.4	Ruminantia: Cattle, Sheep, Deer, and Giraffe	544
12.5.5	Whippomorpha: Hippos, Whales, and Extinct Relatives	546

12.5.6	Cetacea: Evolution of the Whales	547
12.6	Zooamata: Horses, Carnivores, and Pangolins	550
12.6.1	Panperissodactyls	551
12.6.2	The Evolution of Horses	552
12.6.3	Tapirs and Rhinoceroses	554
12.6.4	Brontotheres and Chalicotheres	554
12.6.5	Carnivora: Terrestrial Carnivores	556
12.6.6	Pinnipedia: Aquatic Carnivores	558
12.6.7	Pholidota: The Scale-Covered Pangolins	562
12.7	Glires: Rodents, Rabbits, and Relatives	563
12.7.1	Rodent Teeth and Jaws	563
12.7.2	Rodent Evolution	564
12.7.3	Lagomorpha: Rabbits, Hares, and Pikas	567
12.8	Archonta: Primates, Tree Shrews, and Flying Lemurs	568
12.8.1	Scandentia: Tree Shrews	568
12.8.2	Dermoptera: Flying Lemurs	568
12.9	Ice Age Extinction of Large Mammals	569
12.9.1	Overkill or Climate Change	569
12.9.2	After the Extinction	570
12.10	Further Reading	574
	Questions for Future Research	574
	References	574
13	Human Evolution	585
	Introduction	585
13.1	What Are the Primates?	585
13.2	The Fossil Record of Early Primates	586
13.2.1	Plesiadapiforms	588
13.2.2	Adapiformes: The First Primate Diversification	588
13.2.3	Strepsirrhini: Lemurs and Their Kin	590
13.2.4	Tarsiiformes: Tarsiers and Their Kin	591
13.3	Anthropoidea: Monkeys and Apes	592
13.3.1	Anthropoid Adaptations	592
13.3.2	The First Anthropoids	594
13.3.3	Platyrrhini: The New World Monkeys	595
13.3.4	Catarrhini: The Old World Monkeys	597
13.4	Hominoidea: The Apes	597
13.4.1	Early Ape Evolution	599
13.4.2	Hominidae: First Forms and Orang-utan Evolution	599
13.4.3	Evolution of European and African Hominids	603
13.5	Evolution of Human Characteristics	603
13.5.1	Bipedalism: Humans as Upright Apes	603
13.5.2	Increased Brain Size	604
13.5.3	'Brain-first' Theories of Human Evolution	604
13.6	The Early Stages of Human Evolution	605
13.6.1	The Pre-australopithecines: <i>Orrorin</i> , <i>Sahelanthropus</i> , <i>Ardipithecus</i>	605
13.6.2	Early <i>Australopithecus</i> : Lucy and Her Relations	607
13.6.3	The Later Australopithecines	608
13.6.4	<i>Homo habilis</i> and <i>H. rudolfensis</i> : Transitional Hominins	609
13.7	The Past Two Million Years of Human Evolution	611
13.7.1	Out of Africa I – <i>Homo erectus</i>	611
13.7.2	Middle Pleistocene Hominins	613

- 13.7.3 The Neanderthal Peoples 614
- 13.7.4 Out of Africa II – Modern *Homo sapiens* 616
- 13.8 Further Reading 620
 - Questions for Future Research 620
 - References 620

Appendix: Classification of the Vertebrates 629

Glossary 641

Index 647

List of Boxes

Tree of Life Boxes

Chapter 1	Deuterostome Phylogeny	11
	Rotting Bias	16
	Neural Crest and the Vertebrate Head	19
Chapter 2	Classification	55
Chapter 3	Early Vertebrate Relationships	68
	Origins of Eugnathostomes	89
	<i>Guiyu</i> and the Origin of Bony Fishes	96
	Early Gnathostome Relationships	99
Chapter 4	Phylogeny of the Devonian Tetrapods	121
	Relationships of the Carboniferous Tetrapods	144
Chapter 5	Relationships of Early Amniotes	161
	Relationships of the Synapsid Groups	177
Chapter 6	Explosive Evolution of Marine Predators	205
	Diapsid Diversification	209
Chapter 7	Chondrichthyan Relationships	248
	Early Diverging Actinopterygian Relationships	256
	Relationships of Neopterygii	262
Chapter 8	Relationships of the Dinosaurs	291
Chapter 9	Relationships of Mesozoic Reptiles	351
	The Origin of Snakes	381
Chapter 10	Bird Fingers: 1, 2, 3 or 2, 3, 4?	413
	Relationships of the Earliest Birds	418
	Neognath Relationships	435
Chapter 11	Cynodont Phylogeny	460
	Relationships of Non-Eutherian Mammals	476
Chapter 12	The Phylogeny of Modern Mammals	526
	Dogs: Domesticated Wolves, or What?	559

Chapter 13	Relationships of the Primates	587
	Relationships of Apes and Humans	600
	Neanderthal and Denisovan Genomics	615

Exceptional Faunas and Palaeogeography Boxes

Chapter 1	The Chengjiang Biota	7
Chapter 2	Geological Time	42
Chapter 3	Scanning Galeaspid Heads	78
	Old Red Sandstone Fishes of Scotland	94
Chapter 4	Tetrapods of the Volcanic Springs	130
	Recumbirostrans: Tiny Carboniferous and Permian Burrowers	135
	Life in the Lakes of the Early Permian	141
Chapter 6	Ancient Burrowers	200
	Among the Sea Lily Fields of Guanling	203
	The Marvellous Manda Formation	221
Chapter 7	The Age of Sharks	246
	Miocene Jaws!	253
	Luoping and the Explosion of Triassic Fishes	260
	Coral Reefs Promote Teleost Diversity	274
Chapter 8	Dwarf Dinosaurs on Ancient Islands	308
Chapter 10	Impact of the Jehol Birds	420
	Giant Horse-Eating Birds of the Cenozoic	445
Chapter 11	The First Swimming Mammaliaform	479
Chapter 12	Messel World – Eocene Life	531
	Dead Whales as Long-Term Feeding Stations	550
Chapter 13	The World's First Tarsier	592
	<i>Australopithecus sediba</i> : Transitional Fossil	609

Biomechanics and Behaviour Boxes

Chapter 2	Writing an Abstract	34
	Vertebrate Palaeontology Careers	37
	Engineering the Skull of <i>T. rex</i>	50
Chapter 3	Devonian Jaws: Body Size and Bite Force	84
Chapter 4	Transitional Tetrapod Tomography	125
	The Devil Toad from Madagascar	148

Chapter 5	Weight of the Largest Permian Tetrapod	172
	Dicynodont Diets	184
	Bending Backbones	188
Chapter 6	Archosaur Hindlimb Evolution and Posture	226
	Determining Dinosaur Diets	233
Chapter 7	The First Flying Fish	265
Chapter 8	Swimming Spinosaurids?	296
	Posture Shift in Sauropodomorphs	304
	Aztec Warrior Dinosaur	313
	Hadrosaur Teeth and Success	318
	Dinosaurian Creches and Postural Change	324
Chapter 9	Making an Inside-Out Reptile	345
	Miniature Herbivorous Crocodylians from Madagascar	358
	Pterosaur Flight and Improving Efficiency	365
	Fluid Dynamics and Marine Reptile Swimming	368
Chapter 10	The Colour of Dinosaur Feathers	405
	Giant Penguins	442
Chapter 11	Evolution of Ears	466
	Biting Mechanics of Metatherian and Placental Sabre-Tooths	499
	The Genes for Mammoth Hair Colour	511
Chapter 12	The Shrinking Giant Rodents of South America	566
Chapter 13	The Flores Hobbit	618

Preface

Palaeontology in general, and vertebrate palaeontology in particular, is all about finding new fossils. Or is it? If you rely on newspapers and social media for your news, the reports are mainly about the latest dinosaurs or human fossil finds. These discoveries are massively important of course, and we can celebrate that palaeontologists are active in lands that had not been much explored before, such as China and various countries in Africa and South America. The new fossils expand our knowledge of fossil distributions, and of course, many of them offer remarkable new information. But, as any young palaeobiologist knows, the discovery of new species is a minor concern. Much more exciting has been the blossoming of new computational techniques that extend the reach of studies in macroevolution and palaeobiology further than might have been imagined even ten years ago.

When I wrote the first edition of this book in 1989, I felt that there was a need for an up-to-date account of what is known about the history of vertebrates, but also for a thorough phylogenetic framework throughout, then something of a novelty. The first edition was published in 1990. The second edition, substantially modified, appeared in 1997, the third, extensively rewritten in 2005, and the fourth, further updated and enlarged and with a section of colour plates, in 2015. These new editions offered extensive coverage of new discoveries and new interpretations through the previous 25 years. Between 1990 and 2005, the book hopped from publisher to publisher: it was commissioned by Unwin Hyman, who was soon after acquired by Harper Collins, and their science list was in turn acquired by Chapman & Hall, so the first edition appeared under three publishers' logos, in 1990, 1991 and 1995. The second edition appeared with Chapman & Hall, but they were then taken over by Kluwer, and this book was marketed by their Stanley Thornes subsidiary for a while, before passing to Blackwell Science in 2000, which is now part of John Wiley & Sons. I hope these wandering days are now over.

The first edition appeared in Spanish in 1995 (*Paleontología y evolución de los vertebrados*, Edition Perfil,

Lleida), the second in Italian in 2000 (*Paleontologia dei Vertebrati*, Franco Lucisano Editore, Milano), the third in German in 2007 (*Paläontologie der Wirbeltiere*, Dr Friedrich Pfeil, München), and the fourth in Chinese (*Gǔ jǐchuí dòngwù xué* [*Vertebrate Palaeontology*], Science Press, Beijing, 2017). This is a measure of the international appeal of vertebrate palaeontology and the demand from students and instructors for up-to-date information.

Presenting this new, fifth, edition to the public is hugely exciting for me, for three reasons. First, this marks 35 years in print – ever since 1990 – and I am still beavering on. Second, it is a chance to share an astonishing array of remarkable new research across the field, from the first fossil chordates in the Cambrian to fossil hominids. Third, it is all in colour. Publishing has advanced in leaps and bounds since the last edition, in 2015, and colour is the norm in scientific papers. Young authors take great care in designing the images in their papers, so they are as graphic and informative as possible. This massively helps the textbook writer and reader.

The story of the evolution of the vertebrates, the animals with backbones, is fascinating. There is currently an explosion of new research ideas in the field concerning all the major evolutionary transitions, the origin of the vertebrates, dramatic new fish specimens unlike anything now living, adaptations to life on land, the Triassic revolution when life recovered from the profound end-Permian mass extinction, the origin and radiation of dinosaurs, the evolution and palaeobiology of dinosaurs, the origin and diversification of birds, the earliest mammals, ecology and mammalian diversification, the Paleogene radiation of modern mammalian clades, reconciling morphological and molecular evidence on bird and mammal evolution, and the origins and evolution of human beings.

I have five aims in writing this book. The first aim is to present **a readable narrative of the history of the vertebrates** that is accessible to everyone, with either a professional or an amateur interest in the subject. The book broadly follows the time sequence of major events in the

sea and on land so that it can be read as a continuous narrative, or individual chapters may be read on their own. I have tried to show the adaptations of all major extinct groups, both in words and in images.

The second aim is to highlight **major evolutionary anatomical changes** among vertebrate groups. This book is not a classic anatomy text, and there is no space to give a complete account of all aspects of the hard-part and soft-part anatomy of the major groups. However, I have selected certain evolutionary anatomical topics, such as the vertebrate brain, tetrapod vertebral evolution, posture and gait in archosaurs, and endothermy in mammals, to present an overview of current thinking, including evolutionary and developmental aspects, where appropriate.

The third aim is to show **how palaeobiological information is obtained**. It is important to understand the methods and debates, and not simply to assume that all knowledge is fixed and immutable. Further, science is about testing hypotheses against evidence, not about who shouts loudest, and it is important to realize that even historical sciences, such as palaeontology, can work through hypothesis testing. As an introduction, I summarize in Chapter 2 the methods used by vertebrate palaeontologists in collecting and preparing the fossils, in using them to learn about ancient environments, biomechanics and palaeobiology, and as evidence for discovering parts of the great evolutionary tree of life. Then, throughout the text, I present box features that are divided into three categories: tree of life controversies (deuterostome relationships, jawless fishes, osteichthyans, sarcopterygians, basal tetrapods, amniotes, dinosaurs and the origin of birds, molecular information on mammalian phylogeny, hominin relationships), exceptional fossils or faunas (new exceptionally preserved basal chordates from China, a rich fossil deposit of early tetrapods, exceptional fishes and marine reptiles from the Triassic of China, dramatic new discoveries of Cretaceous birds, fossil mammals with hair, new basal humans from Africa, the Flores ‘hobbit’) and palaeobiology of selected unusual ancient vertebrates (limb mechanics of the first tetrapods, jaw action and diet of dicynodonts, archosaur locomotion, hadrosaur chewing adaptations, flight efficiency in pterosaurs, giant penguins, horse-eating birds, rodents as large as rhinos).

The fourth aim is to survey **the present state of discovery of the tree of life of vertebrates**. The cladograms are set apart from the body of the text, and comprehensive lists of the key diagnostic characters are given. In some cases, there are controversies among palaeontologists, or between the morphological and the molecular results, and these are explored. In many cases, it was a difficult task to represent current views fairly, yet incisively. Some parts of the tree appear to have been relatively stable for ten years or more, whereas others are

changing rapidly – these aspects are indicated. The cladograms throughout the book may be linked to provide an overview of the vertebrate tree of life, and this is replicated in the classification (Appendix).

The fifth aim, which has always been embedded in earlier editions, is to highlight **career development for aspiring palaeontologists**. This is done partly by the emphasis on method: the young palaeontologist, progressing through Bachelors, Masters, and Doctoral degrees, must keep an open and enquiring mind. Learning in detail about the occurrence, anatomy, systematics, and function of a particular group of sharks, dinosaurs, or rodents is clearly crucial, as ever, but now the enthusiastic student must also master reasonably advanced computational protocols in phylogenetic, macroevolutionary, palaeoecological, taphonomic, or biomechanical analysis. Interdisciplinarity is key. The message about career development is stressed also by the choice of current research highlights in the box features: many of these are based on recent publications by young researchers.

I am indebted to many people. I thank †Roger Jones and Clem Earle of Unwin Hyman who commissioned the first edition 35 years ago, Ward Cooper of Chapman & Hall who steered the second edition through, and Ian Francis and Delia Sandford who worked hard on the third and fourth editions for Blackwell and Blackwell-Wiley. The following people read parts of earlier editions, or made other valuable contributions: †Dick Aldridge, Phil Anderson, †Peter Andrews, Kenneth Angielczyk, David Archibald, Chris Beard, Roger Benson, Donald Benton, David Berman, Martin Brazeau, Derek Briggs, Steve Brusatte, Richard Butler, †Henri Cappetta, †Bob Carroll, Luis Chiappe, Brian Choo, †Jenny Clack, Mike Coates, Liz Cook, Joel Cracraft, Ted Daeschler, Brian Davis, Eric Delson, †David Dineley, Phil Donoghue, Gareth Dyke, Greg Edgecombe, Andrzej Elzanowski, Susan Evans, Valentin Fischer, Jens Franzen, Nick Fraser, Matt Friedman, Jörg Fröbisch, Keqin Gao, †Brian Gardiner, †Alan Gentry, David Gower, Lance Grande, †Bev Halstead, David Hone, Jim Hopson, Axel Hungerbühler, Christine Janis, Philippe Janvier, †Dick Jefferies, Tom Kemp, †Zofia Kielan-Jaworowska, Gillian King, Jürgen Kriwet, Adrian Lister, Liz Loeffler, Zhexi Luo, John Maisey, Gerald Mayr, Andrew Milner, Sean Modesto, Jingmai O’Connor, Kevin Padian, †Alec Panchen, Mike Parrish, †Colin Patterson, Kevin Peterson, Davide Pisani, Mark Purnell, Emily Rayfield, Jeremy Rayner, Robert Reisz, Olivier Rieppel, Bruce Rubidge, Lauren Sallan, Rob Sansom, †Bob Savage, Rainer Schoch, Paul Sereno, Koen Stein, Glen Storr, Chris Stringer, Pascal Tassy, Ian Tattersall, Mike Taylor, †Nigel Trewin, David Unwin, Jakob Vinther, †Cyril Walker, †Peter Wellnhofer, Bernard Wood, Feixiang Wu, Xing Xu, and Adam Yates. For the fifth edition, I thank Ken Angielczyk,

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Note Concerning the References

Throughout the book, I refer readers to relevant papers. Most of these are recent, but I include a few older, classic works. There are so many papers on some themes, such as the phylogenetic relationships of particular groups or the biomechanics of dinosaurs, that it is impossible to give a comprehensive, or even a fair listing. I have chosen by preference, short and well-illustrated papers and reviews that should be accessible to students. Indeed, I have tried to favour work by young researchers, especially in the box features – this has the additional purpose of showing students how their contemporaries and near-contemporaries are using their skill and enthusiasm to forge professional careers for themselves around the world.

Note: I would appreciate any corrections (e-mail to mike.benton@bristol.ac.uk). More details are available at <https://www.bristol.ac.uk/earthsciences/research/palaeobiology/research/benton-lab/>.

Michael J. Benton

About the Companion Website

This book is accompanied by a companion website:

www.wiley.com/go/benton/vertebratepalaeontology



The website includes:

- PowerPoints of all figures from the book for downloading

1

Vertebrates Originate

Key Questions in this Chapter

- 1) What are the closest living relatives of vertebrates? Did vertebrates originate as worms or bag-like beasts?
- 2) When did deuterostomes and chordates originate?
- 3) What are the key characteristics of chordates?
- 4) How do embryology and morphology, combined with new phylogenomic studies, inform us about the evolution of animals and the origin of vertebrates?
- 5) How do extraordinary new fossil discoveries from China help us understand the ancestry of vertebrates?

Introduction

Did vertebrates begin as worms or bags? This is the question. There are currently two viable hypotheses for the origin of vertebrates, called more properly the vermiform and the sessile hypotheses (Nanglu et al. 2023a). The vermiform hypothesis is that the ancestral vertebrate was like an enteropneust hemichordate, with a simple nervous system and a gill-slit-laden pharynx. The sessile origins hypothesis is that the ancestral vertebrate was a tentaculate animal that lived in a fixed position on the seabed and was perhaps more like a pterobranch hemichordate or a urochordate. We will look at what all this means, examining these close relatives of vertebrates as well as some spectacular fossils, and then summarize between worms and bags at the end of the chapter.

Vertebrates are the animals with backbones, fish, amphibians, reptiles, birds, and mammals. We have always been especially interested in vertebrates because this is the animal group that includes humans. The efforts of generations of vertebrate palaeontologists have been repaid by the discovery of countless spectacular fossils: heavily armoured fishes of the Ordovician and Devonian, seven- and eight-toed Devonian tetrapods, sail-backed synapsids, early birds and dinosaurs with feathers, giant rhinoceroses, rodents with horns, horse-eating flightless birds, and sabre-toothed cats. These fossils tell us where the living vertebrates have come from, and they show us glimpses of different worlds that are bizarre enough

to defy the imagination of a science fiction writer. Despite all this information that has accumulated over the past 200 years, the origin of vertebrates is still hotly debated.

One thing is clear from the biology of living animals. Vertebrates are members of a larger group, the Phylum Chordata, which also includes their closest living relatives, marine animals such as the sea squirts and amphioxus (see below). These creatures do not have a skeleton, but they share other features, such as a **notochord**, a flexible, tough rod that runs the length of the body along the back. The notochord in living chordates is generally made from an outer sheath of collagen, a tough fibrous connective tissue that encloses turgid, fluid-filled spaces. Invertebrate chordates also have V-shaped muscle blocks (**myomeres**) along the length of their body. The question about the origin of vertebrates then broadens out to include the origin of chordates.

Looked at more widely, vertebrates are a minor twig among Animalia in the 'Tree of Life' (Figure 1.1). It is common to think of the major divisions of life as being animals, plants, protists, and simple organisms classed broadly as bacteria and viruses. Molecular studies (Williams et al. 2020; McGrath 2022) show that all living things evolved from a single last universal common ancestor (LUCA) perhaps 4000 Ma, and then split into two clades, Bacteria and Archaea. Eukaryota then branched from Archaea perhaps 2200 Ma, with some input from symbiotic bacteria to form fundamental cell organelles. The familiar plants, animals, and fungi are

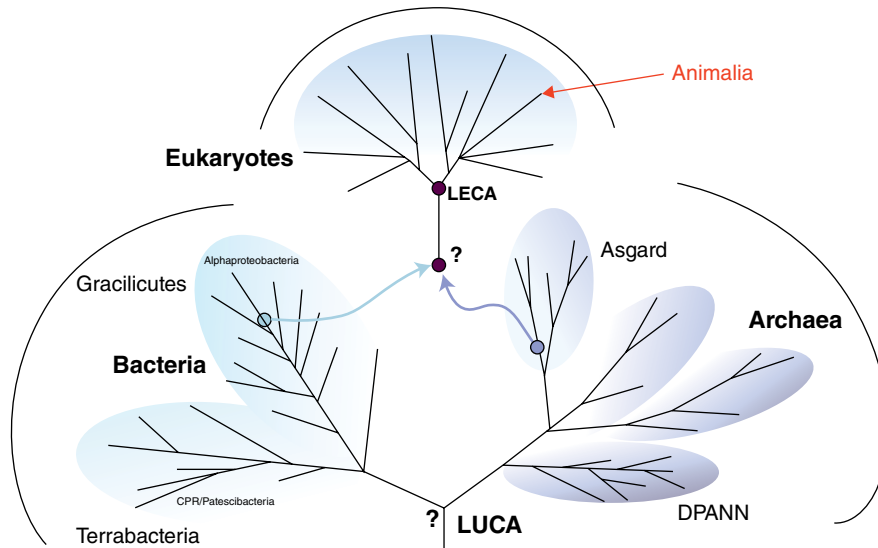


Figure 1.1 The Universal Tree of Life, showing the three main divisions: Eukarya, Archaea, and Eukaryotes. The last universal common ancestor (LUCA) and last eukaryote common ancestor (LECA) are marked. Animals are one of many twigs of the phylogenetic tree. Source: From McGrath (2022), reproduced according to CC BY-4.0 licence.

members of Eukaryota, all diagnosed by complex cells with a membrane-bound nucleus and mitochondria. Within Eukaryota are various protist groups, as well as plants, fungi, and animals, and of course, vertebrates are animals. Among animals, it has always been assumed that chordates are closely related to hemichordates (acorn worms and pterobranch worms) and echinoderms (starfish, sea lilies, and sea urchins), and this is now widely confirmed, based on morphological, developmental, and molecular evidence.

The purpose of this chapter is to explore the various lines of evidence that can be used to reconstruct the origin of the vertebrates: the study of modern animals that are vertebrate-like in some features, the study of molecular relationships, and fossils.

1.1 Sea Squirts and the Lancelet

There are two key groups of living non-vertebrate chordates: cephalochordates (amphioxus) and sea squirts. The amphioxus certainly looks superficially fish-like, but adult sea squirts look like rubbery little bottles, and so would hardly seem to be sensible candidates for close relatives of the vertebrates.

1.1.1 Cephalochordata: Amphioxus

The Cephalochordata (or Acraniata) have long been understood to be close relatives of the vertebrates. The clade includes 30–35 species that live generally in shallow seas of temperate to tropical latitudes, the most famous of which is the amphioxus or lancelet, *Branchiostoma*. The adult

amphioxus is convincingly chordate-like, being a 50 mm-long paperknife-shaped animal that looks like a young lamprey or eel yet lacking a head (Bertrand and Escriva 2011; Holland 2015; Zhang et al. 2018; d’Aniello et al. 2023). Amphioxus swims freely by undulating its whole body from side to side, and it burrows in the sediment on the sea floor (Figure 1.2a, b).

Amphioxus feeds by filtering food particles out of the seawater. Water is pumped into the mouth and through the pharynx by cilia or the gill slits, and food particles are caught up in a bag of mucus produced by the endostyle, the feeding system seen also in tunicates and in the larvae of the lamprey. The mucus with its contained food particles is pulled into the gut for digestion, whereas the seawater passes through the gill slits into the atrium. Oxygen is also extracted, and the wastewater then exits through the **atriopore**.

The anatomy of amphioxus, with its pharynx, notochord, dorsal nerve cord, myotomes, and endostyle (Figure 1.2c) is typically chordate. Swimming and burrowing are done by means of lateral contractions of the myomeres acting against the stiff rodlike notochord.

1.1.2 Urochordata: Sea Squirts

A typical sea squirt, or tunicate, is *Ciona* (Figure 1.3a), which lives attached to rocks in seas around the world. It is a 100–150 mm-tall bag-shaped organism with a translucent outer skin (the tunic) and two openings, or siphons, at the top. *Ciona intestinalis* is one of about 3000 species of urochordates that mostly live in shallow seas, are generally attached to the seabed, and live either a solitary or colonial existence. But the adult sea squirts do not look much like vertebrates.