

Contents

List of Boxes xvii

Preface xxi

About the Companion Website xxv

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 *Pikaia* 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 Lepospondyli 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	<i>Paleothyris</i> and <i>Hylonomus</i>	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 Crocodilians	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	Pterosauriforms: 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 Crocodilians	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 <i>Homo sapiens</i>	616
13.8	Further Reading	620
	Questions for Future Research	620
	References	620

Appendix: Classification of the Vertebrates 629

Glossary 641

Index 647