

VERTEBRATE LIFE

FOURTH EDITION



F. HARVEY POUGH
JOHN B. HEISER
WILLIAM N. MCFARLAND

FOURTH EDITION

VERTEBRATE LIFE



Prentice Hall

Upper Saddle River, New Jersey 07458

Library of Congress Cataloging-in-Publication Data

Pough, F. Harvey.

Vertebrate life / F. Harvey Pough, John B. Heiser, William N.

McFarland,—4th ed.

p. cm.

Includes bibliographical references and index.

ISBN 0-02-396370-0

1. Vertebrates. 2. Vertebrates, Fossil. I. Heiser, John B. II. McFarland, William N. (William Norman). III. Title.

QL605.P68 1996

596—dc20

95-14458

CIP

Acquisitions Editor: *Sheri L. Snavely*

Editor in Chief: *Paul F. Corey*

Editorial Director: *Tim Bozik*

Assistant Vice President of Production and Manufacturing: *David W. Riccardi*

Executive Managing Editor: *Kathleen Schiaparelli*

Assistant Managing Editor: *Margaret Antonini*

Marketing Manager: *Kelly McDonald*

Manufacturing Buyer: *Trudy Piscioti*

Creative Director: *Paula Maylahn*

Cover Designer: *DesignW, Inc./Wendy Helft*

Photo Editor: *Lorinda Morris-Nantz*

Photo Researchers: *Chris Migdoll, Diane Kraut*

Editorial Assistants: *Lisa Tarabokja and Nancy Bauer*

Art Studio: *Academy ArtWorks, Inc.*

Copyediting and Text Composition: *Electronic Publishing Services Inc.*

Cover Art: © *RipTide, Inc. Maxine Fumagalli/Brendan Japantardi*



© 1996 by Prentice-Hall, Inc.

Simon & Schuster / A Viacom Company

Upper Saddle River, New Jersey 07458

All rights reserved. No part of this book may be reproduced, in any form or by any means, without permission in writing from the publisher.

Previous editions copyright © 1979, 1985, 1989 by Macmillan Publishing Company, a division of Macmillan, Inc.

Printed in the United States of America

10 9 8 7 6 5 4 3 2

ISBN 0-02-396370-0

Prentice-Hall International (UK) Limited, *London*

Prentice-Hall of Australia Pty. Limited, *Sydney*

Prentice-Hall Canada Inc., *Toronto*

Prentice-Hall Hispanoamericana, S.A., *Mexico*

Prentice-Hall of India Private Limited, *New Delhi*

Prentice-Hall of Japan, Inc., *Tokyo*

Simon & Schuster Asia Pte. Ltd., *Singapore*

Editora Prentice-Hall do Brasil, Ltda., *Rio de Janeiro*

VERTEBRATE LIFE

F. Harvey Pough

Arizona State University West

John B. Heiser

William N. McFarland

Cornell University

PREFACE

The fourth edition of *Vertebrate Life* contains changes that reflect the extraordinary activity in vertebrate biology during the past two decades. The most pervasive innovations have resulted from the widespread adoption of phylogenetic systematics (cladistics) as the basis for determining the evolutionary relationships of organisms. The emphasis that this system of classification places on the importance of monophyletic groupings has ramifications in many areas of biology. As an objective (although frequently controversial) method that reflects information about the sequence of changes during evolution, cladistics provides an evolutionary framework in which ideas from other biological specialties can be accommodated. As a result, studies of behavior, physiology, and ecology are increasingly being placed in an explicitly evolutionary context, and this common ground has fostered increased interaction among those specialties.

We have retained the cladistic classification introduced in the third edition as the basis for the fourth edition of *Vertebrate Life*, and have included cladograms illustrating the postulated relationships of vertebrates. In doing so, we have tried to reconcile the views of various authorities and point out major areas of disagreement. The cladograms include synopses of the character states on which they are based and citations of the primary sources used. This information will facilitate exploration of different views, and will help faculty and students to modify the phylogenies presented here as new interpretations are published.

As a result of the cladistic perspective of this edition, we have reorganized the treatment of morphology and physiology to emphasize derived characters of vertebrates. Chapter 3 treats embryonic development and morphology, and Chapter 4 presents a parallel treatment of general aspects of vertebrate physiology and homeostasis. Topics unique to particular groups are highlighted in the chapters treating those groups.

Another important change in this edition is an emphasis on conservation, especially the application of basic biological information about organisms in programs of captive husbandry and management of threatened and endangered species. We believe that collaborative work by academic biologists with colleagues from zoos and conservation organizations, a synthesis we call applied organismal biology, offers the best hope for protecting biological diversity. We have provided examples of successes and failures of work of this sort, and have included admittedly speculative proposals for further applications in the hope that students will be attracted to this field.

Literature citations have been brought up to date, with many references from 1990 onward. As before, we have chosen citations on the basis of their helpfulness

to students attempting to enter the literature of the subject; review articles are cited where possible, and recent references are used because students can trace earlier work through them.

The task of reviewing all of vertebrate biology is nearly overwhelming, and would have been impossible without the hours of time that colleagues spent helping us. We are exceedingly grateful to all of them.

Acknowledgments

Writing a book with a scope as broad as this one requires the assistance of many people. We are grateful to the following colleagues for their generous responses to our requests for information and their comments and suggestions:

Mary Allen (The National Zoo), John Baker (The Open University), Carol Beuchat (California State University at San Diego), the late Robert Bouma (Cornell University), Robert Carroll (McGill University), Mark Chappell (University of California at Riverside), Jennifer Clark (University Museum of Zoology, Cambridge University), Neil Clark (Hunterian Museum, University of Glasgow), Michael Coates (University Museum of Zoology, Cambridge University), Andres Collazo (California Institute of Technology), David Crews (University of Texas), Benjamin Dial (Chapman College), James Edwards (National Science Foundation), Carl Ferraris (California Academy of Sciences), Erik Gergus (Arizona State University West), Carola Haas (Virginia Polytechnic Institute and State University), Timothy Halliday (The Open University), David Hillis (University of Texas), Frank Gill (Academy of Natural Sciences, Philadelphia), Larry Herbst (University of Florida), Ronald Heyer (The National Museum of Natural History), William Hillenius (Oregon State University), James Hopson (The University of Chicago), Elliott Jacobson (University of Florida), Christine Janis (Brown University and The University of Chicago), William Layton (Dartmouth College), Amy McCune (Cornell University), Samuel McLeod (University of Southern California), Barbara Moore (Peabody Museum, Yale University), James Murphy (Dallas Zoo), Olav Oftedal (The National Zoo), Charles Oravetz (National Marine Fisheries Service), Gary Packard (Colorado State University), Alan Pooley (Rutgers University), Donald Prothero (Occidental College), David Roberts (Dallas Zoo), Alan Savitzky (Old Dominion University), Gordon Schuett (Arizona State University West), Donna Shaver (National Biological Survey), Barry Sinervo (University of Indiana), Joe Small (Bone Bug), Ellen Smith (University of Washington), J. A. van den Hoover (University of Stellenbosch), Kentwood Wells (University of Connecticut).

Brooks Burr (Southern Illinois University at Carbondale), Margaret Fusari (University of California at Santa Cruz), William Gutzke (Memphis State University), Christine Janis (Brown University and The University of Chicago), Fred Wasserman (Boston University), Jeffrey Carpenter

(Colorado State University), and Margaret Haag (University of Alberta) reviewed the entire text of the third edition and our plans for changes. Their suggestions have shaped nearly every aspect of this book, and we cannot sufficiently express our gratitude for their efforts.

F. Harvey Pough
John B. Heiser
William N. McFarland

BRIEF CONTENTS

PART I Vertebrate Diversity, Function, and Evolution 2

- 1 The Diversity, Evolution, and Classification of Vertebrates 3
- 2 The Origin of Vertebrates 44
- 3 Vertebrate Organ Systems and Their Evolution 63
- 4 Homeostasis and Energetics: Water Balance, Temperature Regulation, and Energy Use 123
- 5 Geography and Ecology from the Cambrian to the Mid-Devonian 160

PART II Aquatic Vertebrates: Cartilaginous and Bony Fishes 166

- 6 Earliest Vertebrates 167
- 7 The Rise of Jawed Vertebrates and the Radiation of the Chondrichthyes 191
- 8 Dominating Life in Water: Teleostomes and the Major Radiation of Fishes 220
- 9 Geography and Ecology from the Mid-Devonian to Late Permian 276

PART III Terrestrial Ectotherms: Amphibians, Turtles, Crocodilians, and Squamates 280

- 10 Origin and Radiation of Tetrapods in the Late Paleozoic 282
- 11 Salamanders, Anurans, and Caecilians 309
- 12 Turtles 356
- 13 Mesozoic Diapsids: Nonavian Dinosaurs, Birds, Crocodilians, and Others 385
- 14 Geography and Ecology of the Mesozoic 445
- 15 The Lepidosaurs: Tuatara, Lizards, Amphisbaenians, and Snakes 451
- 16 Ectothermy: A Low-Cost Approach to Life 497

PART IV Terrestrial Endotherms: Birds and Mammals 520

- 17 Characteristics of Birds: Specializations for Flight 521
- 18 The Ecology and Behavior of Birds 553
- 19 The Synapsida and the Evolution of Mammals 594
- 20 Geography and Ecology of the Cenozoic 620
- 21 Characteristics of Mammals 636
- 22 Endothermy: A High-Energy Approach to Life 683
- 23 Body Size, Ecology, and Sociality of Mammals 711
- 24 Humans as Vertebrates 732

Glossary 773

Subject Index 779

Author Index 793

CONTENTS

Preface v

PART I

Vertebrate Diversity, Function, and Evolution 2

1	The Diversity, Evolution, and Classification of Vertebrates 3
	The Vertebrate Story 3
	The Different Kinds of Vertebrates 4
	Evolution 7
	Variation and Evolution 16
	Earth History and Vertebrate Evolution 27
	Classification of Vertebrates 29
	Traditional and Cladistic Classifications 30
	The Time Course of Vertebrate Diversity and the Effect of Human Population Growth 38
	Summary 41
	References 42
	Box 1-1 Evolving Views of Evolution 10
	Box 1-2 Tempo in Evolution: The Molecular Clock Hypothesis 24
2	The Origin of Vertebrates 44
	The Significance of Similarity and Differences 44
	Some Familiar Facts About Vertebrates 45
	The Basic Vertebrate Body Plan and a Search for the Relatives of the Vertebrates 45
	Environment in Relation to the Origin of Bone 58
	Did Vertebrates Evolve in Marine or in Freshwater Habitats? 60
	Summary 61
	References 62
	Box 2-1 Multiple Views of the Origin of Craniates 53

3 Vertebrate Organ Systems and Their Evolution 63

- The Unity of Vertebrate Structure 63
- Protection, Support, and Movement 73
- Energy Acquisition and Support of Metabolism 86
- Homeostasis 96
- Coordination and Integration 100
- Continuity of Life: The Reproductive System 116
- Summary 121
- References 121

4 Homeostasis and Energetics: Water Balance, Temperature Regulation, and Energy Use 123

- The Internal Environment of Vertebrates 123
- Exchange of Water and Ions 124
- Responses to Temperature 139
- Energy Utilization: Patterns Among Vertebrates 151
- Summary 157
- References 158

5 Geography and Ecology From the Cambrian to the Mid-Devonian 160

- Early History, Changing Environments, and Vertebrate Evolution 160
- The Environment of Early Craniate Evolution 161
- Terrestrial Ecosystems in the Paleozoic 163
- Early Paleozoic Climates 164
- References 165

PART II

Aquatic Vertebrates: Cartilaginous and Bony Fishes 166

6 Earliest Vertebrates 167

- The First Evidence of Craniates 167
- Earliest Known Craniates 172
- Extant Jawless Fishes 183
- Summary 189
- References 189
- Box 6–1 Reconstructing the First Craniates 170
- Box 6–2 Interrelationships of Early Craniates 179

7	The Rise of Jawed Vertebrates and the Radiation of the Chondrichthyes	191
	The First Appearance of Jaws and Unique Gnathostome Characters	191
	Placoderms: The Armored Fishes	195
	Chondrichthyes: The Cartilaginous Fishes	197
	A Second Radiation of Chondrichthyans: Holocephali	217
	Summary	218
	References	218
	Box 7-1 Food for Sharks	208
	Box 7-2 Electoreception by Elasmobranchs	210
8	Dominating Life in Water: Teleostomes and the Major Radiation of Fishes	220
	Living in Water	220
	The Appearance of Teleostomes	238
	The Evolution of the Actinopterygii	242
	Extant Actinopterygii; Ray-Finned Fishes	247
	Actinopterygian Reproduction and Conservation	259
	Sex Reversal and Life History Strategies of Actinopterygians	262
	Extent Sarcopterygii: Lobe-Finned Fishes	265
	Summary	273
	References	274
	Box 8-1 Mauthner Neurons and the Actinopterygian Brain	230
	Box 8-2 The Evolution of Jaw Mechanisms in Actinopterygians	249
	Box 8-3 The Protrusible Jaw	252
	Box 8-4 What a Fish's Ears Tell About Its Life	268
9	Geography and Ecology From the Mid-Devonian to Late Permian	276
	Continental Geography in the Late Paleozoic	276
	Evolution of Terrestrial Ecosystems	276
	Devonian Climates	279
	References	279

PART III

Terrestrial Ectotherms: Amphibians, Turtles, Crocodilians, and Squamates 280

10 Origin and Radiation of Tetrapods in the Late Paleozoic 282

The Earliest Tetrapods 282

Early Tetrapods 283

The Radiation and Diversity of Nonamniotic Paleozoic Tetrapods 292

Amniotes 298

Summary 308

References 308

Box 10–1 Early Feet 290

11 Salamanders, Anurans, and Caecilians 309

Amphibians 309

Diversity of Life Histories of Amphibians 322

Amphibian Metamorphosis 341

Water Relations of Amphibians 343

Poison Glands and Other Defense Mechanisms 346

Why Are Amphibians Vanishing? 349

Summary 353

References 354

Box 11–1 The Energy Cost of Vocalization by Frogs 334

Box 11–2 Eye of Newt and Toe of Frog: Toxins in the Skin of Amphibians 348

12 Turtles 356

Everyone Recognizes a Turtle 356

Phylogenetic Relationships of Turtles 359

Turtle Structure and Functions 359

Ecology and Behavior of Turtles 368

Conservation of Turtles 376

Summary 382

References 383

Box 12–1 High-Tech Hatchlings 372

Box 12–2 Sick Turtles 378

13 Mesozoic Diapsids: Nonavian Dinosaurs, Birds, Crocodilians, and Others 385

The Mesozoic Fauna 386

Phylogenetic Relationships Among Diapsids 387

The Archosauromorpha 388

The Saurischian Dinosaurs and the Origin of Birds	400
The Ornithischian Dinosaurs	413
The Ecology and Behavior of Nonavian Dinosaurs	419
The Lepidosauromorpha: Ichthyosaurs, Lizards, and Others	429
Other Terrestrial Vertebrates of the Late Mesozoic	436
Late Cretaceous Extinctions	438
Summary	440
References	442
Box 13-1 Long Snouted Fish Eaters	392
Box 13-2 Dinosaur Eggs and Nests	426

14 Geography and Ecology of the Mesozoic 445

Pangaea: The World Continent	445
Terrestrial Ecosystems	445
Are Mass Extinctions Periodic?	449
References	449

15 The Lepidosaurs: Tuatara, Lizards, Amphisbaenians, and Snakes 451

The Lepidosaurs	451
The Radiation of Squamates	455
Ecology and Behavior of Squamates	463
Thermoregulation and the Ecology and Behavior of Squamates	486
Summary	494
References	495
Box 15-1 The Way of a Snake	466
Box 15-2 Caudal Autotomy: Your Tail or Your Life	476
Box 15-3 Designer Lizards	484

16 Ectothermy: A Low-Cost Approach to Life 497

Vertebrates and Their Environments	497
Characteristics of Environments	498
Ectotherms in Extreme Environments	499
The Role of Ectothermal Tetrapods in Terrestrial Ecosystems	516
Summary	519
References	519
Box 16-1 Doubly Labeled Water	506

17 Characteristics of Birds: Specializations for Flight 521

Birds as Flying Machines 521

Feathers and Flight 522

Aerodynamics of the Avian Wing Compared to Fixed Airfoils 526

Body Form and Flight 533

The Hind Limbs and Locomotion 541

The Sensory Systems 547

Summary 551

References 551

Box 17-1 High-Flying Birds 538

Box 17-2 Not Hearing Straight: Ear Asymmetry of Owls 550

18 The Ecology and Behavior of Birds 553

The Evolution of Birds 553

Birds as Model Organisms 557

Social Behavior and Reproduction 567

Migration and Navigation 583

Summary 591

References 592

Box 18-1 Giant Predatory Birds 564

Box 18-2 Training Bird Brains 570

Box 18-3 Built-in Babysitters: Nest Helpers 585

19 The Synapsida and the Evolution of Mammals 594

Terrestrial Vertebrates of the Late Paleozoic 594

The Synapsid Skull 595

Eupelycosaurs and Caseasaurs 595

Therapsida and Theriodontia 601

The First Mammals 610

Summary 617

References 618

Box 19-1 The Evolution of the Mammalian Middle Ear 607

20 Geography and Ecology of the Cenozoic 620

Continental Geography During the Cenozoic 620

The Pleistocene Ice Ages 623

Cenozoic Mammals and Vicariance Biogeography 625

Chance in Evolution 633

References 635

21	Characteristics of Mammals	636
	The Major Lineages of Mammals	636
	The Mammalian Integument	637
	Mammalian Food and Feeding Specializations	649
	Evolution of the Mammalian Nervous and Sensory Systems	663
	Mammalian Reproduction	671
	Summary	680
	References	681
	Box 21–1 Herbivores, Microbes, and the Ecology of Digestion	659
22	Endothermy: A High-Energy Approach to Life	683
	Costs and Benefits	683
	Energy Budgets of Vertebrates	684
	Endotherms in the Cold: The Arctic	686
	Migration to Avoid Stressful Conditions	690
	Torpor as a Response to Low Temperatures and Limited Food	692
	Endotherms in the Heat: Deserts	697
	Summary	709
	References	710
	Box 22–1 Waking Up Is Hard Work: The Cost of Arousal	695
	Box 22–2 How Hot Is It?	706
23	Body Size, Ecology, and Sociality of Mammals	711
	Social Behavior	711
	Population Structure and the Distribution of Resources	712
	Advantages of Sociality	717
	Body Size, Diet, and the Structure of Social Systems	718
	Social Systems Among Primates	724
	Summary	730
	References	731
	Box 23–1 Unprofitable Prey?	723
24	Humans as Vertebrates	732
	The Origin of Humans	732
	Evolution and Phylogeny of the Hominoidea	737
	The Human Race and the Future of Vertebrates	753
	Summary	768
	References	769
	Glossary	773
	Subject Index	779
	Author Index	793

VERTEBRATE LIFE