

Dinosaurs A Concise Natural History

FOURTH EDITION

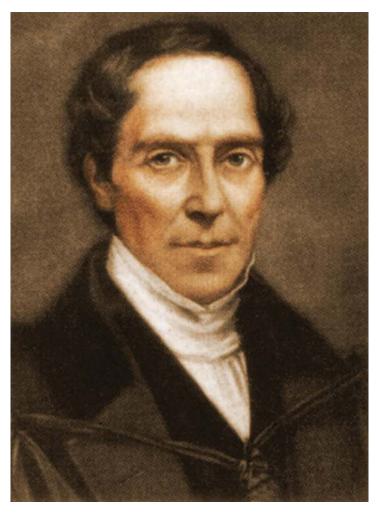
The ideal textbook for nonscience majors, this lively and engaging introduction encourages students to ask questions, assess data critically and think like a scientist. Building on the success of previous editions, *Dinosaurs* has been reorganized and extensively rewritten in response to instructor and student feedback. This edition has been thoroughly updated to include new discoveries in the field, such as the toothed bird specimens found in China and recent discoveries of dinosaur soft anatomy. Illustrations by leading paleontological illustrator John Sibbick and new, carefully chosen photographs, clearly show how dinosaurs looked, lived and their role in Earth history. Making science accessible and relevant through clear explanations and extensive illustrations, the text guides students through the dinosaur groups, emphasizing scientific concepts rather than presenting endless facts. Grounded in the common language of modern evolutionary biology – phylogenetic systematics – students learn to think about dinosaurs the way that professional paleontologists do.

DAVID E. FASTOVSKY is Professor in the Department of Geosciences at the University of Rhode Island. His interest in dinosaurs began in his early years when he read about a paleontologist's adventures in the Gobi Desert early in the twentieth century. Dinosaurs won out years later when he had the tough decision of choosing between a career in music or paleontology. He has since carried out fieldwork all over the world. He is known as a dynamic teacher as well as a respected researcher on the environments in which dinosaurs roamed, as well as their extinction.

DAVID B. WEISHAMPEL is a Professor Emeritus at the Center for Functional Anatomy and Evolution at Johns Hopkins University School of Medicine. His research focuses on dinosaur evolution and how dinosaurs function, and he is particularly interested in herbivorous dinosaurs and the dinosaur record of Europe. He is senior editor of *The Dinosauria* and has contributed to a number of popular publications, including acting as consultant to Michael Crichton in the writing of *The Lost World*, the inspiration for Steven Spielberg's film *Jurassic Park*. He was recently honored in an International Symposium on duck-billed dinosaurs, dedicated to him and his research.

JOHN SIBBICK has been creating illustrations of extinct life forms and their environments for over 30 years, producing numerous books on dinosaurs, as well as pterosaurs, and general books on prehistoric life. His work has appeared in scientific magazines, television documentaries and museums, and featured on a set of stamps depicting dinosaurs and other prehistoric reptiles for the United Kingdom's Royal Mail.





Gideon Mantell (1790–1852), the "father" of modern dinosaur paleontology.



Dinosaurs A Concise Natural History

FOURTH EDITION

DAVID E. FASTOVSKY University of Rhode Island

DAVID B. WEISHAMPELThe Johns Hopkins University School of Medicine

With illustrations by JOHN SIBBICK





CAMBRIDGEUNIVERSITY PRESS

University Printing House, Cambridge CB2 8BS, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314-321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi - 110025, India

103 Penang Road, #05-06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of the University of Cambridge.

It furthers the University's mission by disseminating knowledge in the pursuit of education, learning and research at the highest international levels of excellence.

www.cambridge.org

Information on this title: www.cambridge.org/9781108475945

DOI: 10.1017/9781108567565

© Cambridge University Press 2021

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 2009 Second edition 2012 Third edition 2016 Fourth edition 2021

A catalogue record for this publication is available from the British Library

ISBN 978-1-108-47594-5 Hardback ISBN 978-1-108-46929-6 Paperback

Additional resources for this publication at www.cambridge.org/dinosaurs4.

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.



To Lesley, Naomi, and Marieke, my family.

To poor Robert, because...

To Sarah and Amy.

Thanks for continuing to remind your dad that there are things other than dinosaurs!



TABLE OF CONTENTS

Preface to the Fourth Edition xi

PART I

Remembrance of Things Past 1

1 To Catch a Dinosaur 7

What's in This Chapter 7
Preservation and Fossils 8
Bagging a Dinosaur 13
Collecting 13

Box 1.1 A Dino Named "Sue" 16

Summary 24 Selected Readings 24 Topic Questions 24

2 Dinosaur Days **27** What's in This Chapter 27

When Did Dinosaurs Live (and How Do We Know)? 28
Continents and Climates 33
Climates During the Time of the Dinosaurs 36
Summary 38
Selected Readings 39
Topic Questions 39
Appendix 2.1 Chemistry Quick 'n Dirty 40
Appendix 2.2 Plate Tectonics 41

3 Who's Related to Whom – and How Do We Know? 45

What's in This Chapter 45
Who Are You? 46
Organic Evolution 46
Phylogenetic Systematics – the Reconstruction of Phylogeny 49
Box 3.1 What's in a Name? Cladograms versus Trees 54

Versus Trees 54

Summary 60

Selected Readings 61

Topic Questions 61

Appendix 3.1 What is "Organic Evolution"? 61

4 Who Are the Dinosaurs? 65

What's in This Chapter 65
Finding the History of Life 66
The Beginning 66
Tetrapoda 69
Box 4.1 Fish and Chips 70
Diapsida 78
Box 4.2 What, if Anything, is a
"Reptile"? 78
Dinosaurs 81
Box 4.3 Stance: It's Both Who You Are and
What You Do 83
Summary 84
Selected Readings 85
Topic Questions 85

5 In the Beginning... 87

What's in This Chapter 87
Finding the First Dinosaur 88
Archosauria 88
Early Dinosauria 93
Ornithischia and Saurischia 95
Is Saurischia More Primitive than
Ornithischia? 97
The Evolution of Dinosauria 97
Box 5.1 But What if We've Had it TOTALLY
Wrong for Over a Century? 98
Let the Games Begin! 100
Box 5.2 No Dates; No Rates 102
Feathers 105
Feathers Without Flight 105

PART II

Summary 108

Selected Readings 109

Topic Questions 110

Saurischia: Meat, Might, Muscle, and Magnitude 113

6 Theropoda I 119 Nature Red in Tooth and Claw What's in This Chapter 119



viii

Table of Contents

Theropoda 120 Theropod Lives and Lifestyles 121 Box 6.1 Putting Meat on the Bones... Through "Extant Phylogenetic Bracketing" 133 Thoughts of a Theropod 135 **PART III** Summary 147 Selected Readings 148 Topic Questions 149 7 Theropoda II 151 Meet the Theropods What's in This Chapter 151 Neotheropoda 153 Tetanurae 153 Box 7.1 Will the Real Tyrannosaurus rex Please Stand Up? 161 Summary 177 Selected Readings 177 Topic Questions 178 8 Theropoda III 179 The Origin and Early Evolution Selected Readings 282 of Birds Topic Questions 283 What's in This Chapter 179 Avialae 180 Box 8.1 The Bird is a Word 180 The Mesozoic Avialary 184 Box 8.2 Plus ça Change... 185 Neornithes (Aves) 193 Origin of Avian Flight 196 Box 8.3 Birds as Dinosaurs: at First, not Exactly a Love(bird)fest 197 Summary 204 Selected Readings 207

9 Sauropodomorpha 211

Modern Bird? 206

Topic Questions 206

The Big, the Bizarre, and the Majestic What's in This Chapter 211 Sauropodomorpha 212 "Prosauropods" 214 Sauropoda 217 Reaching for the Stars 223 The Evolution of Sauropodomorpha 230

Appendix 8.1 What Makes a Modern Bird a

Box 9.1 On Again; Off Again: the Checkered Career of Brontosaurus 236

Summary 239 Selected Readings 240 Topic Questions 240

Ornithischia: Armored, Horned, and Duck-Billed Dinosaurs 243

10 Thyreophora 255

The Armor-Bearers What's in This Chapter 256 Thyreophora 256 Eurypoda 257 Eurypoda: Stegosauria 257 Box 10.1 Dino Doggerel 257 Eurypoda: Ankylosauria – Mass and Gas 268 Box 10.2 The Year of the Ankylosaur (at Least in Canada) 274 The Evolution of Thyreophora 278 Summary 281

11 Marginocephalia 285

Bumps, Bosses, and Beaks What's in This Chapter 285 Marginocephalia 286 Marginocephalia: Pachycephalosauria - in Domes We Trust 286 The Evolution of Pachycephalosauria 293 Marginocephalia: Ceratopsia - Horns and All the Frills 296 Box 11.1 Dino Brains 310 The Evolution of Ceratopsia 312 Summary 316 Selected Readings 317 Topic Questions 318

12 Ornithopoda 321

Mighty Mesozoic Masticators What's in This Chapter 321 Ornithopoda 322 Box 12.1 Those Rascals, the Basal Ornithischians! 335 The Evolution of Ornithopoda 337 Summary 340

Table of Contents

ix

Selected Readings 341 Topic Questions 341

PART IV

Endothermy, Endemism, and Extinction 345

13 The Paleobiology of Dinosaurs I 349

What's in This Chapter 349

Paleobiology 350

Dino Breath 350

Dino Brains 351 Dino Bones 352

Tonnage 357

Fleet-Footed... or Flat-Footed 361

Pathologies 363

Zombies 363

Summary 366

Selected Readings 367

Topic Questions 367

14 The Paleobiology of Dinosaurs II 371

Dinosaur Metabolism - Some

Like it Hot

What's in This Chapter 371

The Way They Were 372

Physiology: Temperature Talk 372

Box 14.1 Warm-Bloodedness: to Have and

to Have Hot 373

So What About Dinosaurs? 373

Bone Histology 380

Air Conditioning 382

Stable Isotopes 382

Summary 388

Selected Readings 389

Topic Questions 390

Appendix 14.1 Chain of Fuels 390

15 The Flowering of the Mesozoic 393

What's in This Chapter 393

Dinosaurs in the Mesozoic Era 394

Box 15.1 The Shape of Tetrapod

Diversity 395

Box 15.2 Counting Dinosaurs 398

Plants and Dinosaurian Herbivores 407

Box 15.3 Dinosaurs Invent Flowering

Plants... or at Least Fuel Their Evolution? 414

Summary 415

Selected Readings 416 Topic Questions 416

16 A History of Dinosaur Paleontology

Through the Ideas of Dinosaur

Paleontologists 419

What's in This Chapter 419

In the Beginning 420

Seventeenth and Eighteenth

Centuries 421

Box 16.1 Indiana Jones and the Central

Asiatic Expeditions of the American

Museum of Natural History 422

The Nineteenth Century Through the Mid

Twentieth Century 422

Box 16.2 Sir Richard Owen: Brilliance and

Darkness 424

Dinosaurs in the First Half of the Twentieth

Century 425

Dinosaurs Before Jurassic Park (BJP): the

Second Half of the Twentieth Century

(Most of it Anyway!) 427

Box 16.3 Dinosaur Wars in the Nineteenth

Century: Boxer versus Puncher 428

Box 16.4 Louis Dollo and the Beasts of

Bernissart 430

Box 16.5 "Mr Bones" 432

Box 16.6 Tales of Two Germans 434

Box 16.7 Franz Baron Nopcsa: Politics,

Dinosaurs and Espionage 438

Dinosaurs After Jurassic Park – the Late

1990s 442

Today: Young Turks and Old Turkeys 444

Summary 449

Selected Readings 450

Topic Questions 451

17 The Cretaceous–Paleogene

Extinction 453

The Frill is Gone

What's in This Chapter 453

How Important Were the Deaths of a Few

Dinosaurs? 454

Asteroid Impact! 454

Box 17.1 Extinction 458

Volcanic Eruptions 462

Biological Record of the Latest

Cretaceous 464



x Table of Contents

Box 17.2 Getting Fooled by the Fossil Record: the Signor-Lipps Effect 470 Box 17.3 Dinosaurs: All Wrong for Mass Extinctions 472 Extinction Hypotheses 474 Box 17.4 The Real Reason the Dinosaurs Became Extinct 482 Summary 484 Selected Readings 487 Topic Questions 486

Glossary 487 Index of Subjects 507 Index of Genera 517



PREFACE TO THE FOURTH EDITION

Bigger, Better, and Badder

About 40 years ago, a number of dinosaur specialists inaugurated a revolution in our understanding of dinosaurs. Somehow dinosaurs had languished scientifically although they were big draws in museums, on cereal boxes, and in horror flicks. Perhaps it was because they were thought to be cold-blooded, stupid, and extinct because of it. But that revolution – the "Dinosaur Renaissance" (it was just that, a rebirth) – galvanized paleontologists into what can only be thought of as the greatest makeover in history. A shot in the arm from the movie *Jurassic Park*, itself a product of the Dinosaur Renaissance, and dinosaurs got hot (literally!).

In the 40 years since the Dinosaur Renaissance began, we have learned that they were not crocodile cold-blooded; that they were not slow or stupid; that they did not all go extinct (modern birds are dinosaurs), that many kept nests and raised their babies through dinosaur adolescence; that they lived from Antarctica to the Sahara, and everywhere in between; that they were colorful – and that we can know some of those colors(!); that the sexes showed off to each other; and that when the dinosaurs went extinct, they were killed in the most dramatic and shocking way (un)imaginable: by an asteroid impact with Earth. Dinosaurs got bigger, better, and badder. No wonder people became interested in them!

With so many advances in our understanding of dinosaurs coming so fast, we needed to update our book for our readers. To do this every chapter has been thoroughly revised, a new chapter has been added, and three chapters have been completely rewritten. And with the revisions come all kinds of spectacular new photographs, drawn from all over the world, augmenting the collection of beautiful photographs and drawings commissioned especially for this book that it already had. Most importantly, the book is now up to date. We hope you find the book as rich an experience as we have in writing it.

To the Student

How to Get the Most out of this Book

Dinosaurs: A Concise Natural History Fourth Edition (DCNH IV) is designed to be used with an unusually broad range of levels, from the very inexperienced to the crazy into it.

Organization

It is in its organizational design that DCNH IV is unique. The key is that while each chapter explores each subject in increasing detail, it is *not* necessary to push to the end of each chapter before proceeding to the next; users have considerable latitude regarding how deeply they delve into each subject. The most interested readers will take a more comprehensive approach in each chapter; those not wishing to overload on Dinosauria need not explore the full range of subject matter encompassed within each chapter.



хii

Cambridge University Press 978-1-108-47594-5 — Dinosaurs David E. Fastovsky , David B. Weishampel , Illustrated by John Sibbick Frontmatter More Information

Preface to the Fourth Edition

The book is divided into four consecutive parts, designed to be read sequentially.

Part I – Introductory background scaffolding, including collecting, time, phylogeny, and the position of dinosaurs within the vertebrate biota. Some basic details about plate tectonics and evolutionary biology are also provided; because these are not built into the chapters, they are not necessary to get the flow.

Parts II and III – These are the core of the book. You need to know who dinosaurs are, before you can learn about what they did. Each of the dinosaur group-centered chapters is laid out with parallel organization:

- (1) basic (and brief) taxonomic context;
- (2) paleobiology of the dinosaur group; followed by
- (3) a more detailed evolutionary treatment.

This organization is key, because it allows you to choose how deeply you wish to explore each group. Students with less interest in the details of which dinosaur is related to which other dinosaur (dinosaur systematics) need only go, in each chapter, as far as the sections on dinosaur paleobiology, stopping short of the detailed sections on dinosaur systematics (uniformly entitled in each chapter, "The Evolution of...," signaling the systematic complexity to follow).

Students with greater interest can go deeper into the "Evolution of..." sections, exploring the more detailed cladograms, even assessing, should they so choose, the nature of the diagnostic characters provided for each group. Again, the book is designed to allow readers to choose the level at which they wish to engage with this material.

Part IV – Part IV is more synthetic, and includes paleobiological, and macroevolutionary aspects of dinosaur paleontology. The chapters on the paleobiology (Chapter 13), warmbloodedness (Chapter 14), Mesozoic (Chapter 15), and the dinosaur extinction (Chapter 17) are uniquely comprehensive coverages of these difficult topics; and, as in all chapters throughout this book, they are supported by a significant series of carefully chosen original citations from the primary scientific literature.

Chapter 16 is a history of ideas in dinosaur paleontology. History only has resonance when one knows something about the subject, and so we have put this chapter near the end of the book; that way, when you encounter it, you will remember those ideas from the preceding chapters.

This chapter is *not* about names and dates; rather, it is about the development of ideas – and the people who developed them. Today, there are more active dinosaur paleontologists than have ever before, and so in this chapter we also try to introduce you to a few of them.

Textbooks are expensive, and we mean for our students to get the most out of their investment! We hope that you find this book rewarding, and that we can successfully convey some of the excitement and wonder that all professional paleontologists experience in their careers.

To the Instructor

Dinosaurs: A Concise Natural History is designed to introduce first- and second-year university students, many commonly seeking to fulfill general science requirements, to the logic of scientific inquiry and to concepts in natural history and evolutionary biology. The perspectives and methods introduced through dinosaurs have a relevance that extends far beyond the dinosaurs, teaching scientific logic and critical thinking. The approach has been successful for around 40 years, and new



Preface to the Fourth Edition

xiii

discoveries and interpretations now merit this fourth edition. Professional paleontologists, including even dinosaur specialists, will find in it a comprehensive overview of the group, with many of the key issues highlighted.

In its preparation, Cambridge University Press again devoted considerable energy to obtaining extensive feedback from the many instructors who had had experience teaching from previous editions. The thoughtful, detailed, and, in many cases, comprehensive, answers obtained for this fourth edition were particularly useful in determining the ways in which this edition could be strengthened as a teaching tool. Accordingly, we have responded to virtually all suggestions and recommendations. The care that veteran instructors have put into their answers has surely enriched our book; we are most grateful!

A Unique Conceptual Approach

Names, dates, places, and features are available everywhere these days. But litanies of names, dates, and places is not science; the *creative* synthesis of these data is far more important and, fortunately, far more interesting. The goal of this book is to help students achieve that synthesis.

Reflecting its field, DCNH IV is organized through the lens of phylogenetic systematics. This approach allows students to understand dinosaurs as professional paleontologists do. To have had an entire class in dinosaurs, and yet be insensible to the underlying phylogenetic connections among these (and all) organisms is indefensible; it would be akin to studying biology without evolution. The cladograms used in this book are drawn in a way that highlights the evolutionary relationships they depict, ensuring that both the methods and conclusions of phylogenetic systematics remain accessible.

Part I introduces the fundamental intellectual tools of the trade, including collecting, geological time, the logic of phylogenetic systematics, and enough basic tetrapod anatomy to get the ball rolling. Parts II and III cover, respectively, Saurischia and Ornithischia. The chapters within Parts II and III cover the major groups within Dinosauria, treating them in terms of behavior, lifestyle, and finally evolution. The central role of birds as living dinosaurs is developed through Theropoda I, II, and III. The normally prominent status accorded to *Archaeopteryx* has here been diminished, since the astounding Liaoning fossil discoveries in the past 25 years have undermined the uniqueness of *Archaeopteryx* as a transition to birds. Reflecting this, we've augmented the section on Mesozoic bird evolution, supported by some extraordinary photographs of fossils from the Jehol avian biota, generously donated by Dr. Luis Chiappe and Ms. Stephanie Abramowicz, both of the Natural History Museum of Los Angeles. Ornithischians are treated in Chapters 10 to 12, culminating in Ornithopoda, a group that remains phylogenetically somewhat fraught. By the time students reach this chapter, however, they will be in a position to understand, appreciate, and assimilate some of the uncertainty.

Part IV covers the aspects of the paleobiology of Dinosauria, from their biology (Chapter 13), to their metabolism (Chapter 14), to the great rhythms that drove their evolution (and coevolution; Chapter 15), to a fully updated discussion of their extinction (Chapter 17). Chapter 16, the penultimate chapter, is devoted to a history of dinosaur paleontology. Although commonly introduced at the beginning of dinosaur books, our history chapter (Chapter 16) – a history of *ideas* – is placed toward the end, so that the thinking that currently drives the field can be understood in context. We believe that the history of dinosaur paleontology is much more resonant when students already know something about the fossils being hunted and the ideas being developed. Finally, the book ends, like the dinosaurs themselves, with a discussion of the great Cretaceous–Paleogene mass extinction. Here



xiv Preface to the Fourth Edition

we might say, as so many have, that Earth then entered the Age of Mammals, but, paradoxically, we'll try to persuade readers that we're still in the "Age of Dinosaurs."

We would cheat our readers if we left out accounts of the dinosaur specialists, whose colorful personalities and legendary exploits make up the lore of dinosaur paleontology; so we've included a few of their stories as well (Chapter 16). The fourth edition also highlights Generation X and even a few Millennial paleontologists in the hope that our readers might see something of themselves in these accomplished young professionals.

Finally, as in all previous editions, any errors that appear in this work are entirely Dave's fault.

Features

DCNH IV is designed to help instructors to teach and to help students learn.

- The book continues to be richly illustrated with especially commissioned art by John Sibbick, one
 of the world's foremost illustrators of dinosaurs. We have also dramatically increased the number
 of photographs and, in this new edition, obtained many replacements as well. Cambridge
 University Press now prints the book in color which, we believe, increases the impact of
 its contents.
- As always, the chapters are arranged so that they present the material in order of increasing complexity and sophistication, building the confidence of the student early on, and extending their sophistication gradually as they progress through the book.
- The tone of the text is light, lively, and readable, engaging readers in the science, and dispelling the apprehension many students acquire when they pick up a science textbook.
- Objectives at the beginning of each chapter help students to grasp chapter goals.
- Boxes scattered throughout the book present a range of ancillary topics, from dinosaur poetry, to
 extinction cartoons, to how bird lungs work, to colorful accounts of unconventional, outlandish,
 and extraordinary people and places.
- A comprehensive series of "Topic Questions," to be used as study guides, are located at the end of each chapter. The questions probe successively deeper levels of understanding, and students who can answer all of the "Topic Questions" will have a good grasp of the material. Variants of these questions can serve as excellent templates for examination questions.
- A Glossary ties definitions of key terms into the pages where the terms are used.
- There are two indices: an Index of subjects and an Index of genera, which includes English translations of all dinosaur names.
- Appendices are included in certain chapters to introduce material that students may need in order to understand chapter concepts, such as the chemistry necessary to understand radioactive decay, plate tectonics, the morphology of modern birds, and the basic principles of evolution by natural selection (Darwinian evolution).

Online resources to help you deliver your dinosaur course include:

- electronic files of the figures and images within the book;
- lecture slides in PowerPoint with text and figures to help you to structure your course; and
- solutions to the questions in the text for instructors.

All resources are available to instructors at www.cambridge.org/dinosaurs4.