

David E. Fastovsky • David B. Weishampel

# DINOSAURS

A CONCISE NATURAL HISTORY

Third Edition

# Dinosaurs

## A Concise Natural History

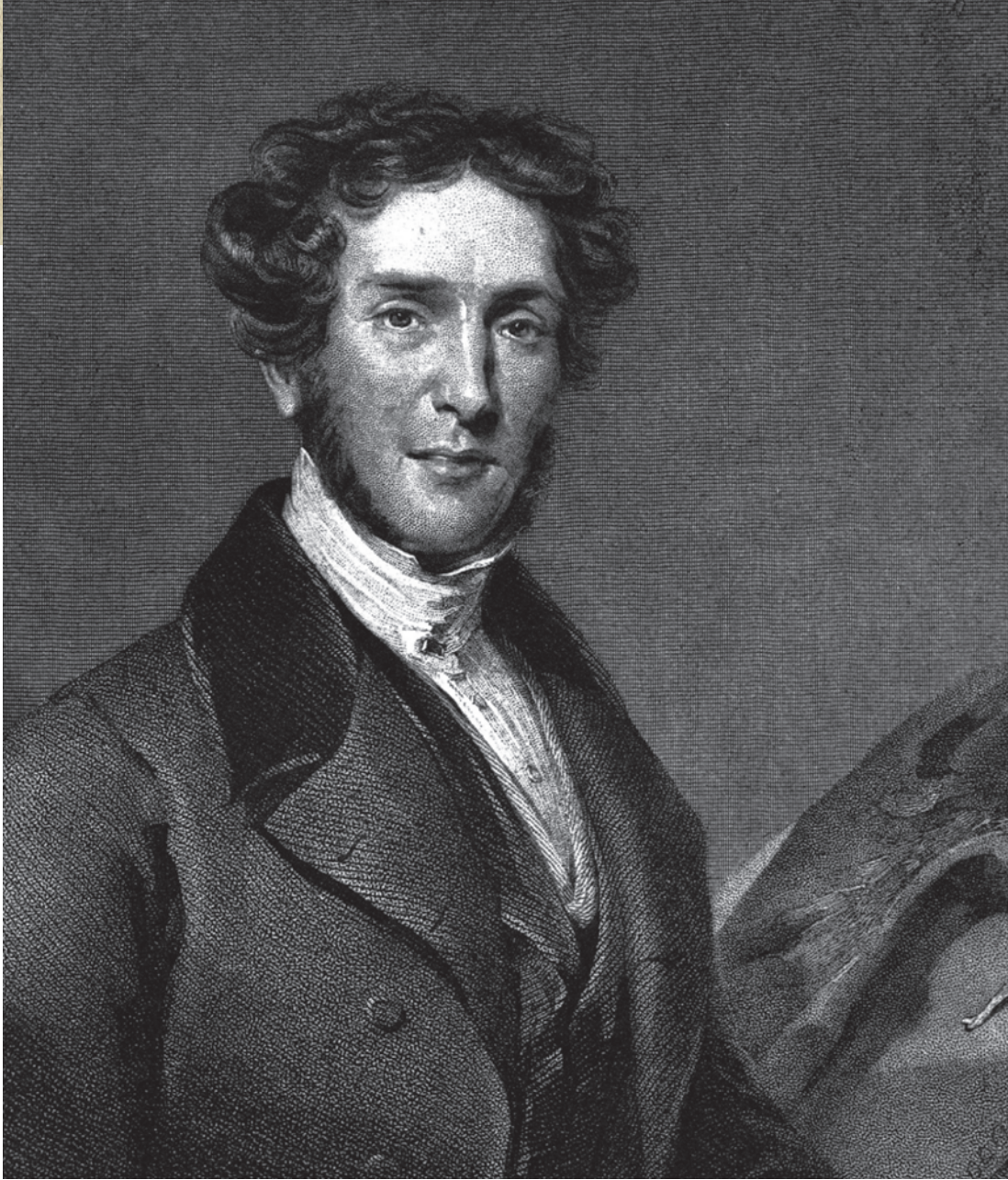
THIRD EDITION

The ideal textbook for non-science majors, this lively and engaging introduction encourages students to ask questions, assess data critically and think like a scientist. Building on the success of the previous editions, *Dinosaurs* has been reorganized and extensively rewritten in response to instructor and student feedback. It continues to make science accessible and relevant through its clear explanations and extensive illustrations. Updated to reflect recent fossil discoveries and to include new taxa, the text guides students through the dinosaur groups, emphasizing scientific concepts rather than presenting endless facts. It is grounded in the common language of modern evolutionary biology – phylogenetic systematics – so that students examine dinosaurs as professional paleontologists do. The key emerging theme of feathered dinosaurs, and the many implications of feathers, have been integrated throughout the book, highlighted by the inclusion of stunning new photographs in this beautifully illustrated text, now in full color throughout.

**DAVID FASTOVSKY** is Professor and Chair of the Department of Geosciences at the University of Rhode Island. His interest in dinosaurs started as a child 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 (he takes his viola on his many field trips) or paleontology, and he has carried out fieldwork all over the world. He's 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 Professor in the Center for Functional Anatomy and Evolution at The Johns Hopkins University School of Medicine. His research focuses on dinosaur evolution and how dinosaurs functioned, and he is particularly interested in herbivorous dinosaurs and the dinosaur record of Europe. Among his many publications 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 well 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, plus a set of stamps depicting dinosaurs and other prehistoric reptiles for the United Kingdom's Royal Mail.



Frontispiece. Gideon Mantell (1790–1852), the “father” of modern dinosaur paleontology.

# Dinosaurs

## A Concise Natural History

THIRD EDITION

**DAVID E. FASTOVSKY**

*University of Rhode Island*

**DAVID B. WEISHAMPEL**

*The Johns Hopkins University*

With illustrations by **JOHN SIBBICK**



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# PREFACE TO THE THIRD EDITION

Non-bird dinosaurs (“dinosaurs”) are very much in the news these days: dinosaurs had feathers; dinosaurs were warm-blooded; dinosaurs were snuffed out in mere seconds; we’ve just discovered the largest dinosaur ever; we’ve just discovered the smallest dinosaur ever; here is *Jurassic World*, there is *The Good Dinosaur*. . . it’s a media blizzard. And why not? Ideas about dinosaurs have moved conceptually far beyond the twentieth century: a few weirdo reptiles that lived on this planet, but were too stupid to survive. Today dinosaurs are recognized as centerpieces of vertebrate evolution; they’re just a whole lot more *interesting* than they used to be!

On the one hand, our book is written to help sort out who’s who and what’s what in this barrage of things dinosaurian; on the other hand, and more significantly, our book is written as an introduction to how scientists in general, and natural historians in particular, think about scientific problems.

So what has changed in this third edition? The answer is, a lot; most of it driven by the many exciting discoveries and ideas that have shaped an understanding of dinosaurs since the second edition was published. Even the very number of dinosaurs known has almost trebled just since we began our careers in paleontology, and with things moving forward so quickly, we must keep up.

## This new edition:

- contains the newest discoveries as well as new scientific hypotheses; these include feathers and feather *colors* in ornithomirans, new insights into the origin of dinosaurs, lots of new dinosaurian faces, many new (and updated) cladograms, and a gorgeous bestiary of feathered Chinese dinosaurs that has rewritten the origin of birds;
- has over 50 new illustrations, including many photographs shot especially for this book;
- includes newly modified versions of existing illustrations, for increased clarity;
- is for the first time printed in full color, to show the photographs and hand-drawn artwork to best advantage;
- is heavily rewritten, reorganized, and expanded to encompass improved treatments of dinosaur warm-bloodedness and the significance of feathers, a revised look at dinosaur–plant co-evolution, enlarged discussion of the insights gotten through geochemistry and CT-scanning, and an introduction to some stand-out members of the younger generation of paleontologists. In fact, every chapter has been thoroughly revised and, in some cases, completely rewritten; and
- is completely reorganized, reflecting the newest ideas about the origin and subsequent evolution of dinosaurs.

For all that, however, the book retains its essential qualities:

- it is unique among dinosaur textbooks designed for non-majors, because it introduces and exclusively uses the language and methods of professional paleontologists;

- multiple perspectives and hypotheses are presented; science, of course, doesn't consist of immutable answers;
- the beautiful J. Sibbick illustrations continue to grace its pages; and
- it still contains the same lively style, aimed at clear, understandable explanations of dinosaurs and their world.

### To the student:

We've written DCNH to introduce you to dinosaurs, amazing creatures that last lived 66 million years ago! We'd also like to use these magnificent beasts to give you insights into natural history, evolution, and the ways that scientists study Earth history.

There are all kinds of questions you can ask about dinosaurs. Simple examples include: Were they really that stupid? Did they die all at once overnight? What were the horns for? Did the mothers take care of their babies? Was *T. rex* really nasty? Were all dinosaurs covered with feathers? What color were they? Could *Brontosaurus* run? How fast? Along with getting answers to these and many other questions, you'll also meet legendary and charismatic dinosaur hunters, younger and older (including the original models for *Raiders of the Lost Ark*'s Indiana Jones and *Jurassic Park*'s Alan Grant). DCNH will help you think like a scientist, while your knowledge of dinosaurs, natural history, and science grows with each chapter you read.

The authors, D. E. Fastovsky and D. B. Weishampel, are active dinosaur researchers, with a combined experience of almost 80 years of studying dinosaurs in the field and at universities. The book is enriched by the gorgeous original artwork of John Sibbick, one of the world's best and most famous dinosaur illustrators.

**DAVID E. FASTOVSKY** is Professor and Chair of Geosciences at the University of Rhode Island; he has also taught about dinosaurs and Earth history at the University of California (Berkeley), the National Autonomous University of Mexico and at the University of Vienna. His interest in dinosaurs started as a child when he read about Roy Chapman Andrews in the Gobi Desert (whose story you'll find in the pages of the book you are holding). Fastovsky has had many of his own adventures in far-flung parts of the world, including France, Argentina, Mexico, Venezuela, the western USA and Canada, and Mongolia. He is known as a dynamic teacher and a respected researcher with a focus on the extinction of the dinosaurs, as well as the environments in which they roamed. He has made several television documentary appearances, and was a recipient of the Distinguished Service Award from, and is a Fellow of, the Geological Society of America.

**DAVID B. WEISHAMPEL** is Professor in the Center for Functional Anatomy and Evolution at The Johns Hopkins University. Recipient of two teaching awards, Weishampel teaches human anatomy, evolutionary biology, cladistics, and, of course, a course on dinosaurs. His research focuses on dinosaur evolution and how dinosaurs function, and he is particularly interested in herbivorous dinosaurs and the dinosaur record of eastern Europe and Mongolia. He is the senior editor of the immensely well-received *The Dinosauria*, and has written or co-written, not including the DCNH series, four books and a many scholarly articles. Weishampel has contributed to a number of popular publications as well, including acting as consultant to Michael Crichton in the writing of *The Lost World*, the inspiration for Steven Spielberg's film *Jurassic Park*. In 2011, a special symposium on duck-billed dinosaurs was convened by the Royal Ontario and Royal Tyrrell Museums, Canada, to honor Dr. Weishampel's contributions to dinosaur paleontology.

**JOHN SIBBICK** has over 35 years of illustration experience working on subjects ranging from mythology to natural history and is probably best known for his depictions of prehistoric scenes and

dinosaurs. In the first stage of any commission he takes the fossil evidence and consults with specialists in their field and works out a number of sketches to build up an overall picture of structure, surface detail, and behavior. From his base in the United Kingdom, he has provided images for books, popular magazines such as the *National Geographic*, and television documentaries, as well as museum exhibits and one-man shows of original artwork. For this book he has provided around 250 pieces of original art.

### 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, engendering in students scientific logic and critical thinking. The approach has been successful, and new discoveries and interpretations now merit this third edition.

In its preparation, Cambridge University Press devoted considerable energy to obtaining extensive feedback from many instructors who had had experience teaching from previous editions. Their thoughtful, detailed, and, in many cases, comprehensive, answers were particularly useful in determining the ways in which this edition could be strengthened as a teaching tool; indeed, we responded, whenever possible, to all suggestions and recommendations. The care that this group of veteran instructors put into their answers has surely enriched our book.

### A unique conceptual approach:

Names, dates, places, and features are available everywhere these days. But litany 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.

Uniquely among dinosaur textbooks, phylogenetic systematics is immanent in DCNH. This approach, however, follows current practice in evolutionary biology, and 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 strikes us as indefensible; it would be akin to studying biology without evolution. The cladograms used in this book are thus 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. Chapters 1 and 2 treat geology, the geological time scale, fossils, collecting, and what happens after the bones leave the field. The third chapter, a carefully crafted introduction to the logic of phylogenetic systematics, uses familiar and common examples to acquaint students with the method. Chapter 4 takes students, phylogenetically, from basal Vertebrata to Dinosauria.

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 phylogeny and evolution, behavior, and lifestyle. For the first time in the DCNH series, this edition puts Saurischia ahead of Ornithischia: this organization allows students to move smoothly from basal (non-dinosaur) dinosauromorphs to the earliest dinosaurs, whose affinities are clearly saurischian, although perhaps murky within that group (Chapter 5). Birds (Chapter 8) follow from the theropod chapters (6 and 7), because birds are living saurischians. In this edition, the normally prominent status accorded to the

venerable *Archaeopteryx* has been diminished, since the astounding Liaoning fossil discoveries in the past 20 years have diminished the uniqueness of *Archaeopteryx* as a transition to birds. In recognition of the close relationship between dromaeosaurs and avialans (including birds), we introduce the group Paraves for the first time in this new edition. Ornithischians are treated in Chapters 10–12, culminating in Ornithomimidae, a group that, with the new millennium, has been 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 metabolism (Chapter 13), to the great rhythms that drove their evolution (and co-evolution; Chapter 14), to a fully updated exposition on their extinction (Chapter 16). Chapter 15, the penultimate chapter, is devoted to the history of dinosaur paleontology. Although commonly introduced at the beginning of dinosaur books via a scaffolding of names, dates, and discoveries,<sup>1</sup> our history chapter – 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 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 hunters, whose colorful personalities and legendary exploits make up the lore of dinosaur paleontology; so we've included many of their stories as well (Chapter 15). In the first and second editions of DCNH, we transparently introduced our own generation as “Young Turks;” forgetting that, like everybody else, we've aged too! The third edition, therefore, introduces its readers to a younger (thirties and forties) generation of paleontologists whose striking accomplishments bode well for their future achievements.

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

## Features:

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

- The book is richly illustrated with new, especially commissioned, art by John Sibbick, one of the world's foremost illustrators of dinosaurs. These images effectively highlight and reinforce the concepts in the text. Many pages are also graced by photographs, generously contributed by professional paleontologists or taken especially for this edition.
- 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 the sophistication of their learning gradually through the book.
- The tone of the text is light, lively, and readable, engaging the student in the science, and dispelling the apprehension many students experience 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, places, and stories.
- 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

<sup>1</sup> Indeed, many of our respondents requested this.

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 page numbers where the term is used.
- There are two indices: an Index of subjects and an Index of genera that 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, 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/dinosaurs3](http://www.cambridge.org/dinosaurs3).



# DEDICATION

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!





# PART I

## REMEMBRANCE OF THINGS PAST

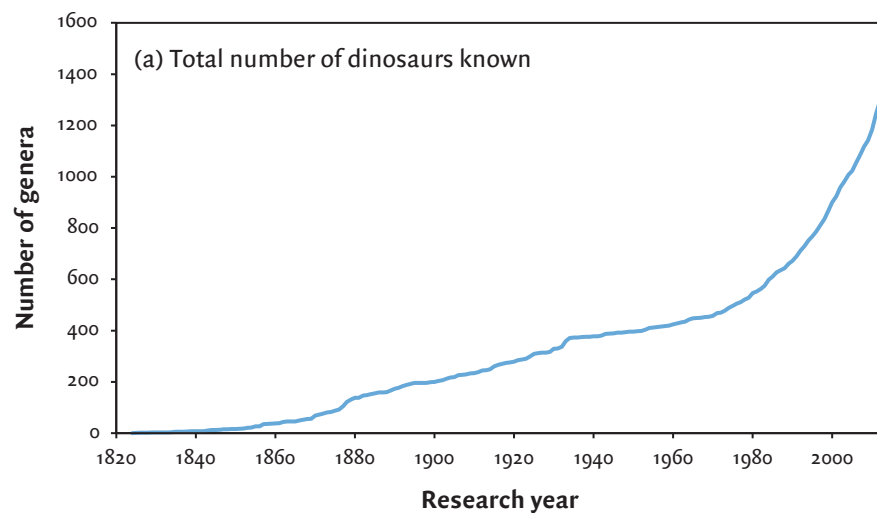


## Dinosaur tales

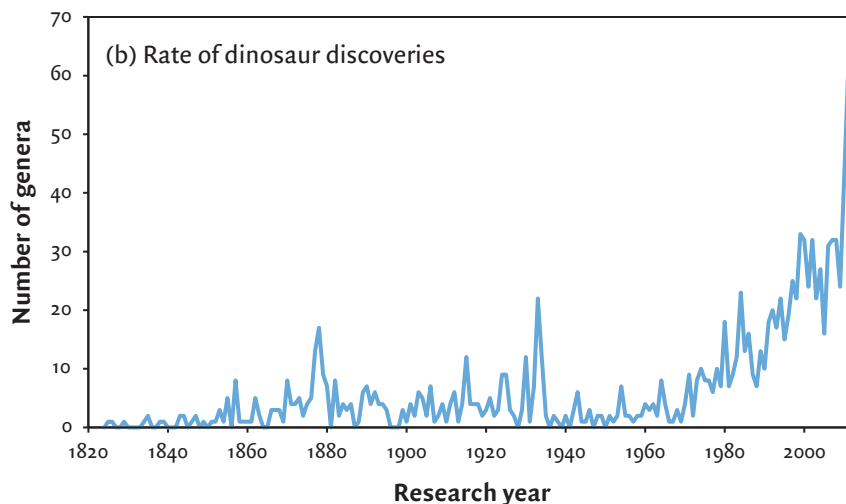
This book is a tale of dinosaurs; who they were, what they did, and how they did it. But, more significantly, it is also a tale of natural history. Dinosaurs enrich our concept of the **biosphere**, the three-dimensional layer of life that encircles the Earth. Our biosphere has a 3.8 *billion*-year history; we, and all other life around us, are merely Earth's latest tenants. To be unaware of the history of life is to be unaware of our organic connections to the biosphere and ultimately to our Earth. Dinosaurs have significant lessons to impart in this regard, because as we learn who dinosaurs really are, we can better understand who *we* really are.

Since the first dinosaur bones were identified in the early nineteenth century, both the total number of dinosaurs known, and the rate of finding them, has spiraled (Figure I.1).

Not only that; it is clear that they are no longer your parents' cast-iron clunkers. Their relationships to us are not what we thought; their lifestyles are not what we thought; they look very different from what we'd imagined; indeed, almost everything about them has changed since the late 1960s and, thankfully, they're a whole lot more interesting now. It seems as if we truly are in a Golden Age of Dinosaur Discovery!



**Figure I.1** Paleontologist Michael Benton's compilation of dinosaur discoveries from 1822 to 2014. (a) Total number of dinosaurs known; (b) rate of dinosaur discoveries. There were spikes in the rate of dinosaur discoveries in the late 1880s and in the early to mid twentieth century, but all of that pales in comparison to the present. As recently as the previous generation of paleontologists, dinosaurs were not so well understood as was thought!



### The word “dinosaur” in this book

The term “dinosaur” (*deinos* – terrible; *sauros* – lizard) was invented in 1842 by the English naturalist Sir Richard Owen (see Box 15.2) to describe a few fossil bones of large, extinct “reptiles.” With modifications (for example, not all dinosaurs are “large”), the name has proven resilient. It has become clear in the past 25 years, however, that not all dinosaurs are extinct; in fact, almost all specialists now agree that *birds are living dinosaurs*. The technically correct term **non-avian dinosaurs** to specify all dinosaurs except birds is a mouthful, so we prefer to use the term “dinosaurs” as shorthand for “non-avian dinosaurs.” The distinction between non-avian dinosaurs and all dinosaurs will be most relevant only when we discuss the origin of birds and their early evolution in Chapters 8 and 9; there, we’ll take care to avoid confusing terminology.

## Science

Ours is also a tale of science, which is in turn all about imagination and creativity, with a little help from data. Creativity is the currency of science; the value of the science is surely dependent upon the creativity of the scientist. In the following pages, we hope to build a sense of the intellectual richness of science; a quality that philosopher of science Karl Popper called the “logic of scientific discovery.” And so if this is a story about science, we’d better articulate what we mean by the word “science.”

### Science = testing hypotheses

*Science is the business of constructing testable hypotheses and then testing them.* An example of a simple scientific hypothesis is: “The Sun will rise tomorrow.” This hypothesis makes specific predictions. Most importantly, the hypothesis that the Sun will rise tomorrow is **testable**; that is, it makes a prediction that can be assessed. The test is relatively straightforward: we wait until tomorrow morning and either the Sun rises or it doesn’t.

So what’s *not* science? Important questions that you can’t get at using science might be “Is there a God?”, “Does she love me?”, and “Why don’t I like hairy men?” In *Music Man*, Marian “the librarian” Paroo asks “What makes Beethoven great?” She won’t learn it from science. Some questions are far better suited to science than others.

### The “proof” is in... the test!

In our example of a scientific hypothesis (above), if the Sun does not rise, the statement has been *falsified*, or demonstrated to be not correct, and the hypothesis can be rejected. On the other hand, if the Sun rises, the statement has *failed falsification*, and the hypothesis cannot be rejected. For a variety of relatively sophisticated philosophical reasons, scientists do not usually claim that they have *proven* a statement to be true; rather, the statement has simply been tested and not falsified. It turns out that, in a philosophical sense, it is very difficult to “prove” anything. For this reason, scientists rarely use words like “prove” or “true” when discussing their work.

But we *can* test hypotheses, and one of the basic tenets of science is that it consists of hypotheses that have predictions which can be tested. We will see many examples of hypotheses in the coming chapters; to be valid, all must involve testable predictions. Without testability, it may be very interesting; it may be very exciting, but it is not science.

### Science in the popular media

“Science” is everywhere in the popular media, from Animal Planet to *National Geographic*, to the Weather Channel. That’s good; our lives are increasingly intersected by science, and the more savvy

we are scientifically, the better the decisions that we can make. But the problem is that not all of the “science” that one sees in the popular media is very scientific!

Among scientists, work is recognized and accepted only after it is **peer-reviewed**; that is, when it has been vetted and carefully scrutinized by other scientists qualified to evaluate the work. Very commonly, the work goes through multiple cycles of review and revision by the authors in response to the critiques of professionals in the field. At that time – and only at that time – it can be published. This is the time-honored – and time-proven – way of producing the very highest quality scientific research.

In the popular media, the goals are somewhat different. In movies, on television, and on the radio, the goals are generally entertainment as well as immediacy: publicizing the newest discoveries as quickly as possible. Both of these have very little to do with high-quality science. In the case of immediacy, the rush to publicize can mean that half-baked theories and interpretations are popularized long before they have seen anything like peer review. And when peer review finally comes, the results can be (and have been) devastating.

The goal of entertainment can be equally destructive, in terms of the science. For example, television and radio reports commonly present “the other side” of a particular scientific issue, even when the vast preponderance of scientists take a particular position and the “other side” has very little legitimacy. People can always be found who will voice heterodox opinions, even when their views are plainly way outside of the mainstream of peer-reviewed science. It’s always *entertaining* to present controversy.

In paleontology, the quest for entertainment brings a variety of excesses, beyond mere controversy. Size sells; teeth and claws sell; asteroids sell; extinction sells. But ultimately, we hope in this book to show that the real riches – and entertainment – lie in a balanced, undistorted treatment of dinosaurs: a more magnificent, fascinating group of creatures could hardly have been invented, and the ongoing scientific process of revealing who they were and what they did is compelling drama.

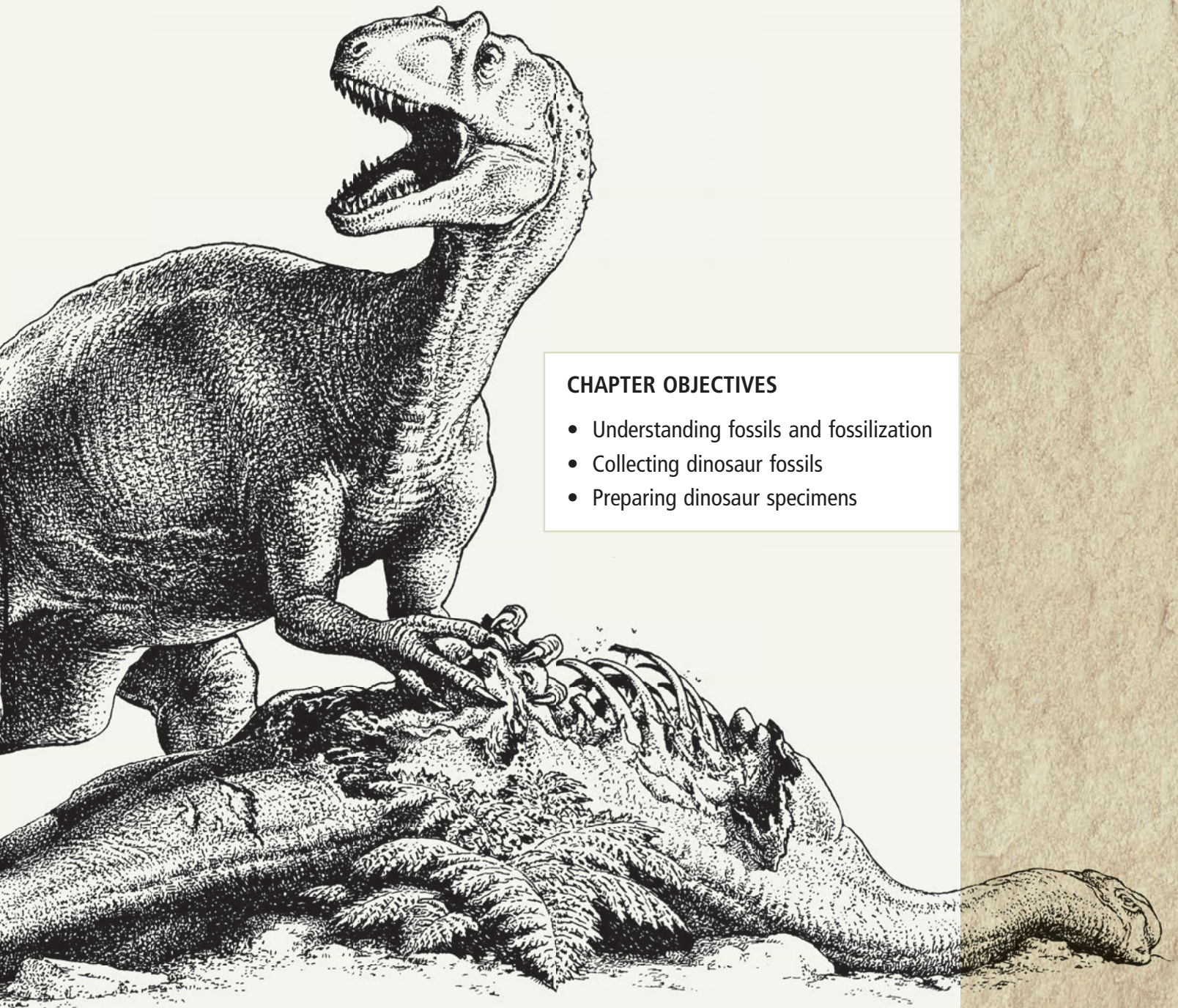
The web, a popular and extremely important source of information, is driven by a variety of sometimes-contradictory imperatives (knowledge; entertainment; retail), and our relationship to it is more nuanced. Accessibility, ease, and breadth are its great strengths; reliability and depth can be, but as always, care about sources is required. Much really good, peer-reviewed science (and lots of other information!) is available on the web; indeed, most major peer-reviewed journals have a significant web presence; some can be found *only* on the web. Information from the websites of professional societies (for example, the Society of Vertebrate Paleontology) is reliable in the way that the peer-reviewed journals published by such societies are reliable. Academic institutions tend to have reliable web pages; although personal web pages, even in an academic context, generally reflect the opinions of their authors, idiosyncratic or not. Wikipedia – a stupendous tool for research and, in our view, a stunning contribution to the availability of human knowledge, reflects the web: it is often very accurate, but it is not without idiosyncratic entries. In short, the web is a powerful tool, to be sure; but *caveat emptor*: Not all sources of information are equivalently authoritative.





# To catch a dinosaur

# 1



## CHAPTER OBJECTIVES

- Understanding fossils and fossilization
- Collecting dinosaur fossils
- Preparing dinosaur specimens



## Preservation and fossils

That we even know there ever were such creatures as dinosaurs is near-miraculous: throughout their time on Earth, a few individuals of the innumerable dinosaurs that must have once lived, happened to be preserved as **fossils**, the buried remains of organic life. There are many types of fossils: most familiar are **body fossils**, which commonly involve some part of the animal (e.g., bones). **Trace fossils**, impressions such as footprints, are also familiar. Finally, there are a variety of **other** kinds of fossils, including things as disparate as molecules and skin impressions.

Dinosaurs last romped on Earth ~66 million years ago, and until the very latest part of the twentieth century, paleontologists mostly assumed that dinosaur **soft tissues** – muscles, blood vessels, organs, skin, fatty layers, etc. – were long gone, with the only observable vestiges being the **hard parts**: generally, bones and teeth. Hard parts were presumably not as easily degraded over time as the soft tissues that constitute most of the body. Yet as it turns out, new techniques and determined study are revealing all kinds of preservation in unexpected places, including tissues, cells, and molecules (for example, the discovery of actual red blood cells and connective tissues from *Tyrannosaurus*; see Box 6.3). Fair warning: it's no longer just about old bones, and we'll visit some of these newer discoveries throughout this book.

### Making body fossils

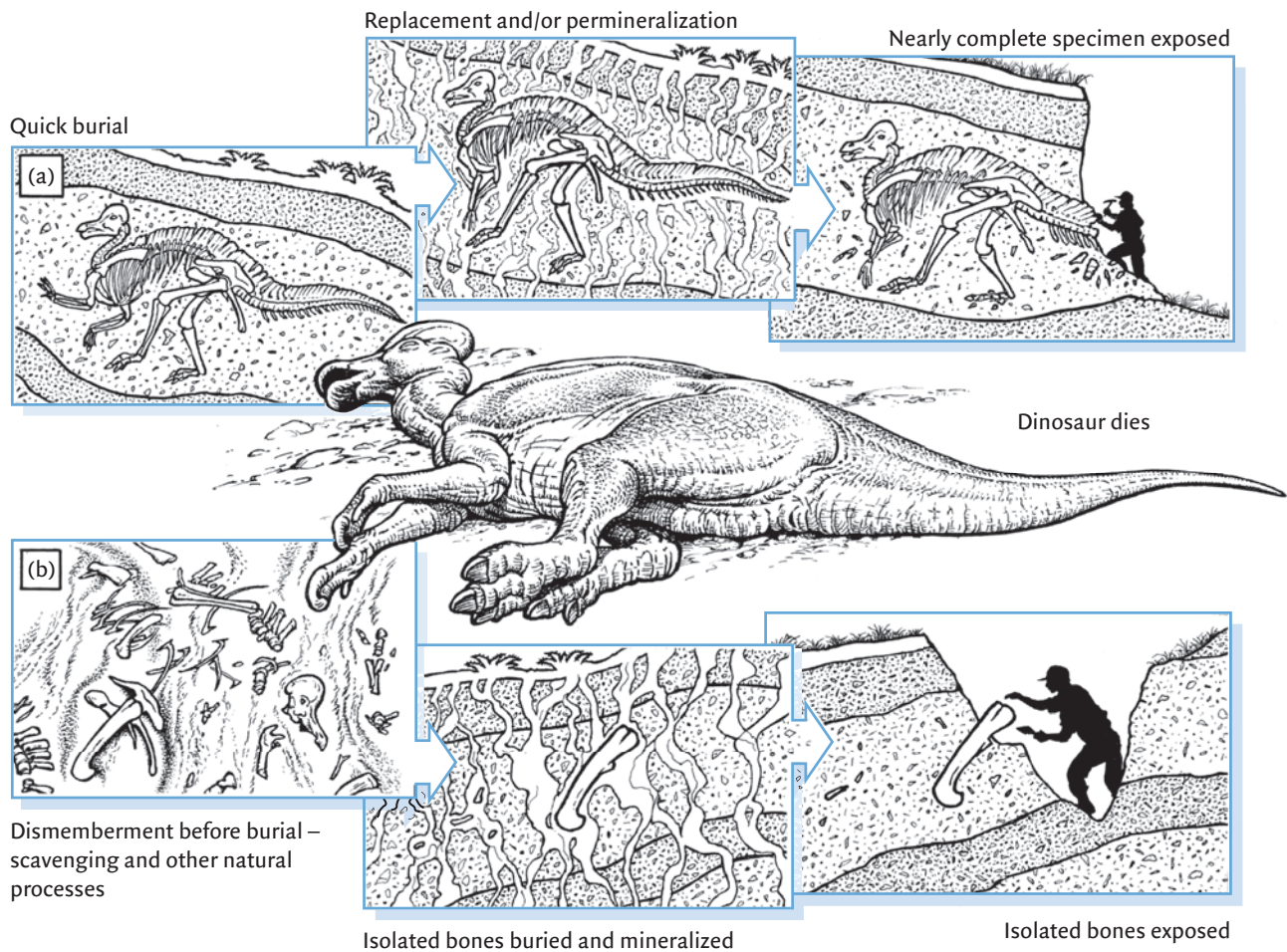
#### Before burial

Consider what might happen to a dinosaur – or any land-dwelling vertebrate – after it dies (Figure 1.1).

Carcasses are commonly **disarticulated** (dismembered), first by predators and then by scavengers ranging from mammals and birds to beetles and bacteria. Some bones might be stripped clean of meat and left to bleach in the sun. Others might get carried off and gnawed. Sometimes the disarticulated remains are trampled by herds of animals, breaking and separating them further. Plants produce acids that dissolve bone. But ultimately, the nose knows that most of the heavy lifting in the world of decomposition is done by bacteria that feast on rotting flesh. The sum total of all the earthly remains of the animal will end up lying there: a few disarticulated bleached bones in the vegetation (Figure 1.1).



**Figure 1.1. Bones.** A wildebeest carcass, partly submerged in mud and water and on its way to becoming permanently buried and fossilized. If the bones are not protected from scavengers, air, and sunlight, they decompose rapidly and are gone in 10–15 years. Bones destined to become high-quality fossils must be buried soon after the death of the animal.



**Figure 1.2.** Two endpoint processes of fossilization. In both cases, the first step is the death of the animal. Some decomposition occurs at the surface. In the upper sequence (a), the animal dies, the carcass undergoes quick burial, followed by bacterial decomposition underground, and permineralization and/or replacement. Finally, perhaps millions of years later, there is exposure. Under these conditions, when the fossil is exhumed, it is largely complete and the bones articulated (connected). This kind of preservation yields bones in the best condition. In the lower sequence (b), the carcass is dismembered on the surface by scavengers and perhaps trampled and distributed over the region by these organisms. The remains may then be carried or washed into a river channel and buried, replaced, and/or permineralized, eventually to be finally exposed perhaps millions of years later. Under these conditions, when the fossil is exhumed, it is disarticulated, fragmented, and the fossil bones may show water wear and/or the gnaw marks of ancient scavengers. Different conditions of fossil preservation tell us something about what happened to the animals after death.

If the animal isn't disarticulated right away, it is not uncommon for a carcass to bloat, as feasting bacteria produce gases that inflate the dead body. After a bit, the carcass will likely deflate (sometimes explosively), and then dry out, leaving bones, tissues, ligaments, tendons, and skin crusty and inflexible.

**Burial**

Sooner or later bones are either destroyed or buried. If they aren't gnawed and digested as somebody's lunch, their destruction can come from **weathering**, which means that the minerals in the bones break down and the bones wash away. But the game gets interesting for paleontologists when weathering is stopped by rapid burial. At this point, they (the bones, not the paleontologists) become fossils. Figure 1.2 shows two of the many paths bones might take toward fossilization.



**Figure 1.3.** Permineralized bone from the Jurassic-aged Morrison Formation, Utah, USA. The fossilized bone is now a solid piece of rock.

### After burial

The burial environment is not chemically static, and the *bad* news is that bone is made out of calcium–sodium hydroxyapatite, a mineral that is not terribly stable on the Earth’s surface. As a result, the original bone minerals are easily **replaced** by other minerals, commonly retaining the details and form of the bone. This is especially likely if the bone comes into contact with fluids rich in dissolved minerals, such as commonly occurs after burial. The *good* news is that, by few choice cation substitutions while buried, calcium–sodium hydroxyapatite commonly alters to more stable forms of apatite, a familiar one being fluorapatite.

If no fluids are present throughout the history of burial (a time interval that could be measured in millions of years), the bone may be unreplaced, which is to say that 100% of the original bone mineralogy remains. On the other end of the spectrum, a completely replaced bone is a magnificent natural forgery: chemically and texturally not bone, but retaining the exact shape and delicate features of the original bone. Given burial stays measured in tens of millions of years, however, most dinosaur bones are altered (replaced) to a greater or lesser degree. Alteration/replacement tends to be progressively greater in the case of older and older fossils; degrees of alteration are generally the norm.

Since bones are porous, the spaces once occupied by blood vessels, connective tissue, and nerves easily fill up with minerals. This is called **permineralization** (Figure 1.3).

Most fossil bones undergo a combination of some degree of replacement and permineralization.

The preceding description explains how isolated fossil bones, or perhaps most of a single animal, might come to be preserved. But along with these isolated finds, on rare and lucky days, we can sometimes come upon **bonebeds**, rich finds with hundreds – even thousands – of bones preserved. Sometimes, these bonebeds are **monospecific**, that is, they contain fossils of mostly one species, and one can’t help but wonder if these perhaps reflect some kind of **gregarious**, or herding behavior captured in the fossil record.

## Trace and other kinds of fossils

### Trace fossils

Still the single most important type of dinosaur fossil, other than the bones themselves, is trace fossils. Dinosaur trace fossils (sometimes also called **ichnofossils** [*ichnos* – track or trace]), come as **footprints** or as complete **trackways**. Figure 1.4 shows a **mold**, or impression, of a dinosaur footprint. We also find **casts**, which are made up of material filling up the mold. Thus a cast of a dinosaur footprint is a three-dimensional object that formed inside the impression (or mold).



**Figure 1.4.** Theropod dinosaur footprint from the Early Jurassic Moenave Formation, northeastern Arizona, USA. Human foot for scale.

In the past 20 years the importance of ichnofossils has been recognized. Ichnofossils have been used to show that dinosaurs walked erect, to reveal the position of the foot, and to reconstruct the speeds at which dinosaurs traveled. Trackways tell remarkable stories, such as that fateful day 150 or so million years ago when a large predatory theropod stalked a herd of smaller animals (Figure 1.5).

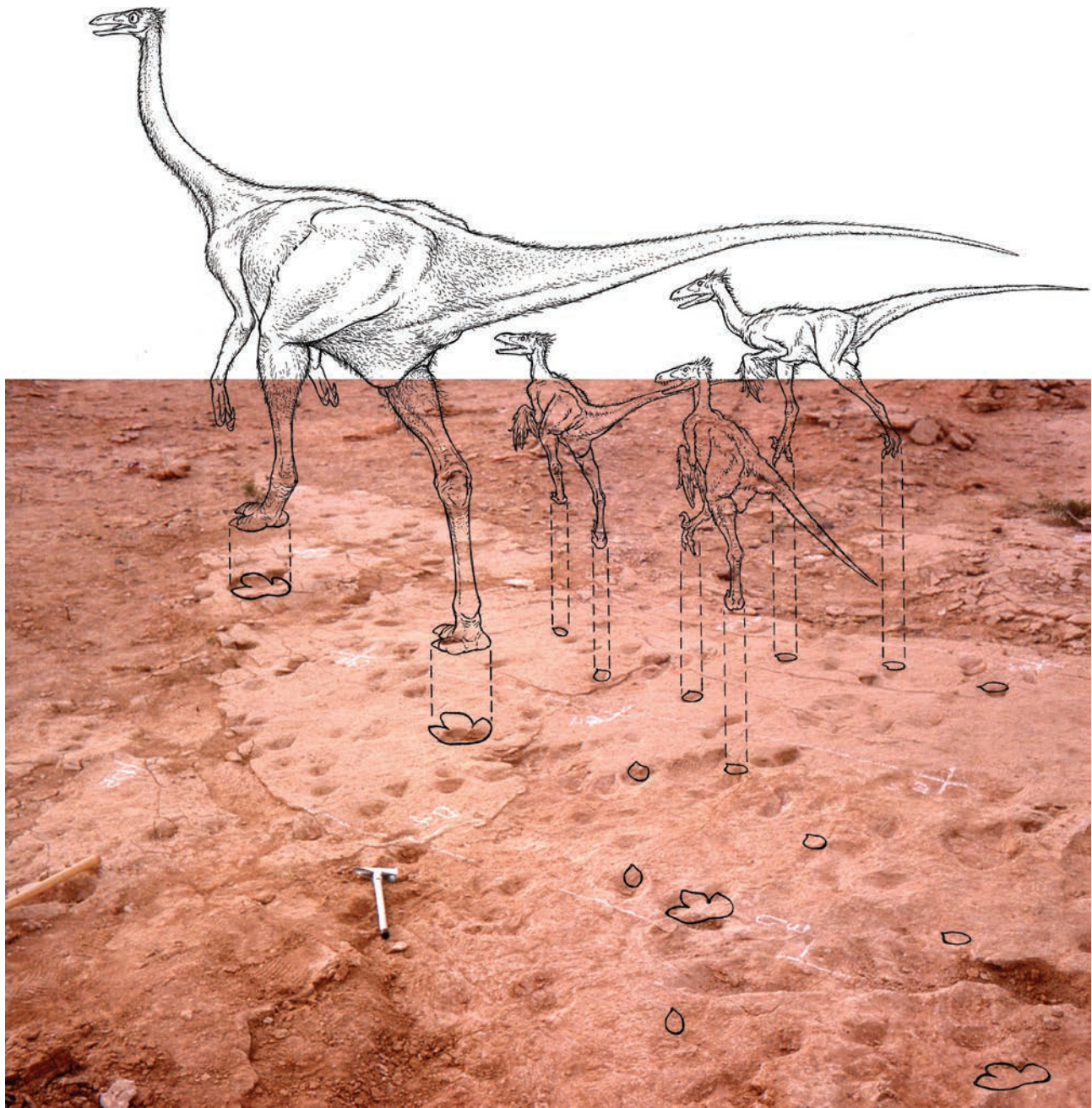
### Other fossils

For want of a more imaginative name, we'll lump the various other kinds of fossils under "Other." Sometimes the fossilized feces of dinosaurs and other vertebrates are found. Called **coprolites**, these occasionally impressive relics can give an intestine's-eye view of dinosaurian diets. Likewise, as we shall see later in this book, fossilized eggs and also skin impressions have been found. Nests are also known (Figure 1.6). Molecules; cells; stomach stones (**gastroliths**; see Figure 6.20); soft tissue; the list is really as long as there are parts of a dinosaur!

### Finding fossils

So, if the fossils are buried, how is it that we find them? The answer is really in the luck of geology: if fossil-bearing **sedimentary rocks** happen to be eroded, and a **paleontologist** happens to be looking for fossils at the moment that one is actively eroding from a rock, the fossil *may* be observed and *may* be collected. Who knows how many times, throughout their 160+ million-year existence on Earth, dinosaurs stepped on exposed, weathering fossils of earlier dinosaurs, now surely lost to eternity (Figure 1.7)?

It's a tenuous connection: the vagaries of fossil preservation, the chance of geological exposure, and their discovery by an ambitious paleontologist. And yet they're out there – the fossils and the paleontologists!



**Figure 1.5.** Photograph from Shar-tsav, Gobi Desert, Mongolia, showing the tracks of a medium-sized theropod dinosaur among those of a pack of smaller theropods. Our drawing suggests an interpretation consistent with the evidence: a *National Geographic* moment in the Late Cretaceous when a pack of *Velociraptor* attacked a single *Gallimimus*.

## Collecting

The romance of dinosaurs is bound up with collecting: exotic and remote locales, heroic field conditions, and the manly extraction of gargantuan beasts (see Chapter 15). But ultimately dinosaur collecting is a process that draws upon good planning, a strong geological background, and a bit of luck. The steps are:

- (1) **planning**;
- (2) **prospecting**; that is, hunting for fossils;
- (3) **collecting**, which means getting the fossils out of whichever (usually remote) locale they are situated; and
- (4) **preparing** and **curating** them; that is, getting them ready for viewing, and incorporating them into museum collections.

These steps involve different skills and sometimes different specialists.

## Planning

Collecting dinosaur fossils is not to be undertaken lightly. Dinosaur bones are – even in the richest sites – quite rare, and the moment they are disturbed the loss of important information becomes a concern. For this reason, most professional paleontologists have advanced degrees – often a PhD in the geological or biological sciences – but before actually leading an expedition themselves, *all* have acquired many years of experience both in the logistical as well as the scientific ends of fieldwork.

### Running an expedition

The logistical end of an expedition involves keeping one's team fed, watered, healthy, and happy in remote places where, in many cases, these commodities don't come easily. Relentless sun, extreme heat, dust, lack of amenities, subsistence on a limited diet, and isolation from the "real world," all conspire to wear down even the most robust of people. It's all happening in the Great Outdoors, true, but it's nothing like a camping catalog! Add to these, language problems when you are working in other countries and limited access to medical facilities in the event of an accident involving either you or one of your crew, and the potential for disaster increases dramatically.

Many expeditions have to carry everything with them – fuel, water, food, all gear for the maintenance of daily life – as well as all the maps and equipment necessary to successfully carry out the science and safely retrieve heavy, yet delicate, dinosaur bones. This takes some serious planning and experience; you and your crew's lives may depend upon it (Figure 1.8). You have to know what you are doing.

Fossils generally, and dinosaurs in particular, are not **renewable resources**, which means that collecting a dinosaur is a one-shot deal: it must be done right, because we will never be afforded another chance to do it again. Any information that is lost – any piece of it that is damaged – may be lost or damaged forever. For this reason, there are many regulations associated with collecting vertebrate fossils.

The most basic are the collection permits required for work on public lands. Obtaining the permits requires advanced planning because the agencies in charge of issuing the permits reasonably require detailed accounts of your plans before the process can go forward.

One important part of the permit-obtaining process, especially in the case of dinosaur fossils (which tend to be large and heavy), is the eventual location of the fossils. Who gets them? Does



**Figure 1.6.** Fossil burrow of the dinosaur *Oryctodromeus*. Careful study of the sedimentary context of this dinosaur revealed the burrow.