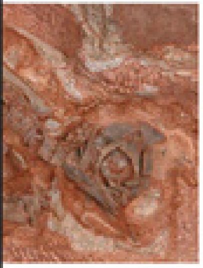

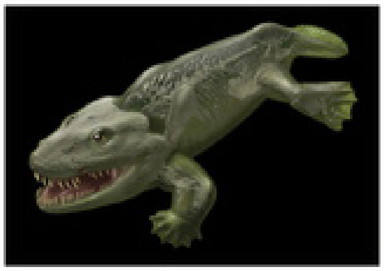


Michael J. Benton · David A. T. Harper

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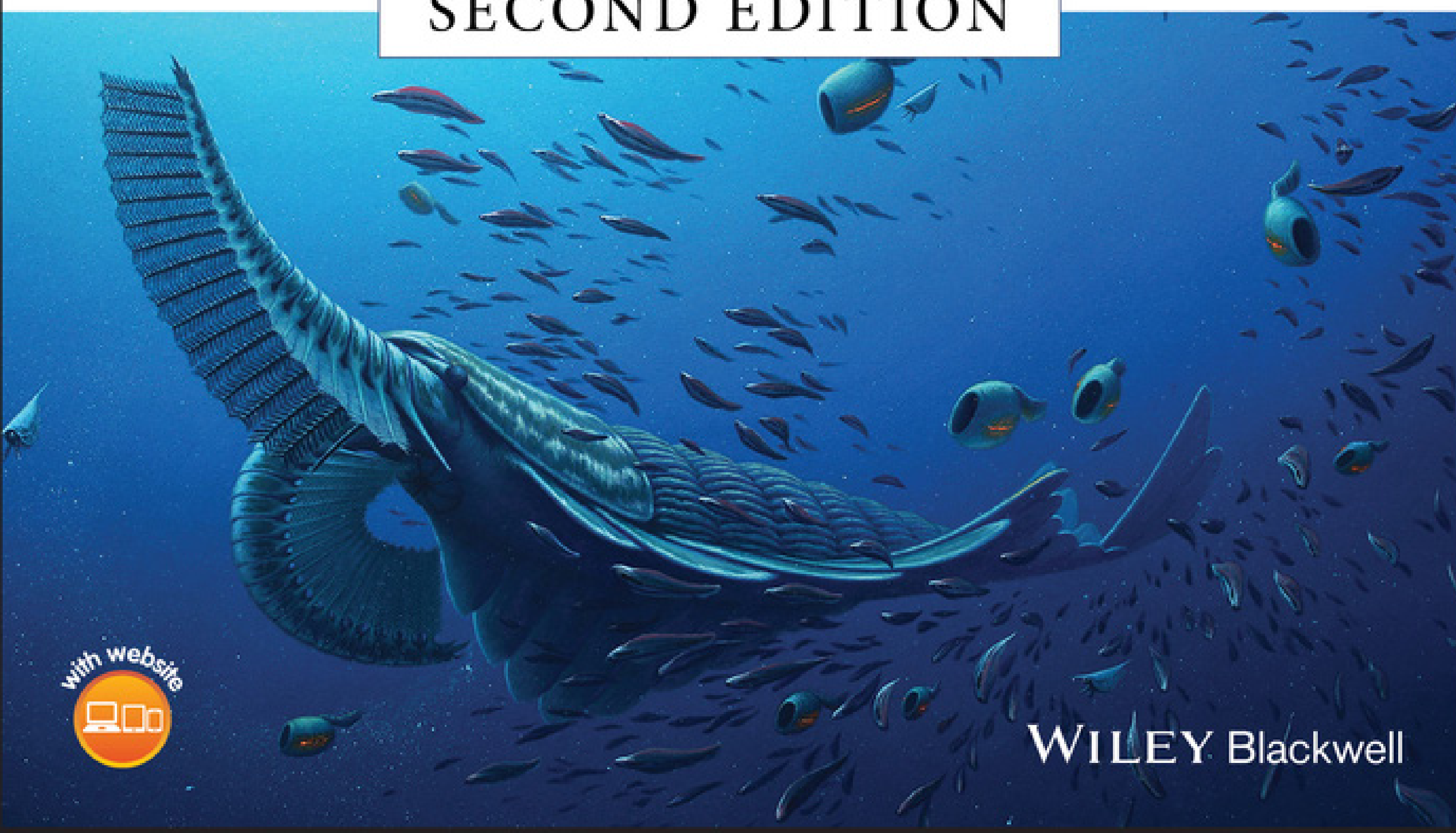

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Introduction to Paleobiology and the Fossil Record

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SECOND EDITION

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WILEY Blackwell

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Preface

The history of life is documented by fossils through the past 3.5 billion years. Paleobiology provides a unique long-term perspective, which is important for three reasons: ancient life and environments can inform us about global change and the origins of modern biodiversity, and so provide information about how the world might change in the future; extinct plants and animals make up 99% of all species that ever lived, and so we need to know about them to understand the true scope of the tree of life; and extinct organisms did amazing things that no living plant or animal can do, and we need to explore their capabilities to assess the limits of form and function.

Every week, astonishing new fossil finds are announced – the world's largest dinosaur from Argentina, new human remains from the caves of South Africa, an elephant from the United States, the oldest fishes from the Cambrian of South China. You read about these in the newspapers, but where do these stray findings fit into the greater scheme of things? Studying fossils can reveal the most astonishing organisms, many of them more remarkable than the wildest dreams (or nightmares) of a science fiction writer. Indeed, paleontology reveals a seemingly endless catalog of alternative universes, landscapes, and seascapes that look superficially familiar, but which contain plants that do not look quite right, animals that are very different from anything now living.

The last 50 years have seen an explosion of paleontological research, where fossil evidence is used to study larger questions, such as climate change, mass extinctions, origins of modern biodiversity, high-precision dating of sedimentary sequences, the paleobiology of dinosaurs and Cambrian arthropods, the structure of Carboniferous coal-swamp plant communities, ancient molecules, the search for oil and gas, the origin of humans, and many more. Paleontologists have benefited enormously from the growing interdisciplinary nature of their science, with major contributions from geologists, chemists, evolutionary biologists, physiologists, and even geophysicists and astronomers. Many areas of study have also been helped by an increasingly quantitative approach.

There are many paleontology texts that describe the major fossil groups or give a guided tour of the history of life. Here we hope to give students a flavor of the excitement of modern paleontology. We present all aspects of paleontology, not just invertebrate fossils or dinosaurs, but fossil plants, trace fossils, macroevolution, paleobiogeography, biostratigraphy, mass extinctions, biodiversity through time, and microfossils. Where possible, we show how paleontologists tackle controversial questions, and highlight what is known, and what is not known. This shows the activity and dynamism of modern paleobiological research. Many of these items are included in boxed features, some of them added at the last minute, to show new work in a number of categories, indicated by icons (see below for explanation).

The book is intended for first- and second-year geologists and biologists who are taking courses in paleontology or paleobiology. It should also be a clear introduction to the science for keen amateurs and others interested in current scientific evidence about the origin of life, the history of life, mass extinctions, human evolution, and related topics. We want to show also the great potential of paleobiology as a career choice for enthusiastic young women and men who are keen to question and debate, and apply novel field, laboratory, and numerical methods to exploring the life of the past.

TYPES OF BOXES

Throughout the text you will find special topic boxes. There are five types of boxes, each with a distinguishing icon:

- Hot topics/debates
- Paleobiological tool
- Exceptional and new discoveries
- Quantitative methods
- Cladogram/classification

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Michael J. Benton
David A. T. Harper
January 2020

About the Companion website

This book includes a companion website at:

The URL is **www.wiley.com/paleobiology**

The website includes:

- An ongoing database of additional Practicals prepared by the authors
- Figures from the text for downloading

Chapter 1

Paleontology as a science

Key points

- The key value of paleontology has been to show us the history of life through deep time – without fossils this would be largely hidden from us.
- Paleontology has strong relevance today in understanding our origins, other distant worlds, climate and biodiversity change, the shape and tempo of evolution, and in dating rocks.
- Paleontology is a part of the natural sciences, and a key aim is to reconstruct ancient life.
- Reconstructions of ancient life have been rejected as pure speculation by some, but careful consideration shows that they too are testable hypotheses and can be as scientific as any other attempt to understand the world.
- Science consists of testing hypotheses, not by limiting itself to absolute certainties like mathematics.
- Classical and medieval views about fossils were often magical and mystical.
- Observations in the sixteenth and seventeenth centuries showed that fossils were the remains of ancient plants and animals.
- By 1800, many scientists accepted the idea of extinction.
- By 1830, most geologists accepted that the Earth was very old.
- By 1840, the major divisions of deep time, the stratigraphic record, had been established by geological fieldwork and the use of fossils.
- By 1840, it was understood that fossils changed through time, and by 1860 this had been explained by evolution.
- Research in paleontology has many facets, including finding new fossils and using quantitative methods to answer questions about paleobiology, paleogeography, macroevolution, the tree of life and deep time.

Introduction to Paleobiology and the Fossil Record, Second Edition. Michael J. Benton and David A. T. Harper.

Companion website: http://www.wiley.com/paleobiology

INTRODUCTION

Paleontology has had a long history, and yet astonishing new discoveries are made all the time. There is a mix of old and new in paleontology; it is a subject with a history of accumulating knowledge over 200 years coupled with the application of modern technology to exploring some of the most fundamental questions about Earth and life. We think of the new discoveries, dinosaur and bird fossils from China, human remains from Africa, and new Precambrian and Cambrian fossils that tell us something about the origin of life and the origin of animals. But new methods are probably more important in advancing our understanding of questions about origins, about extremes in plant and animal life, and about the coupled history of Earth and life through many changes in climate and physical conditions.

In paleontology, difficult questions are often asked about the reconstruction of ancient plants and animals. Surely no one will ever truly know what color dinosaurs were, what noises they made? How could a paleontologist work out how many eggs *Tyrannosaurus* laid, how long it took for the young to grow to adult size, or the differences between males and females? How could anyone discover how an ancient animal hunted, how strong was its bite force, or even what kinds of prey it ate? Surely it is all speculation because we can never go back in time and see what was happening?

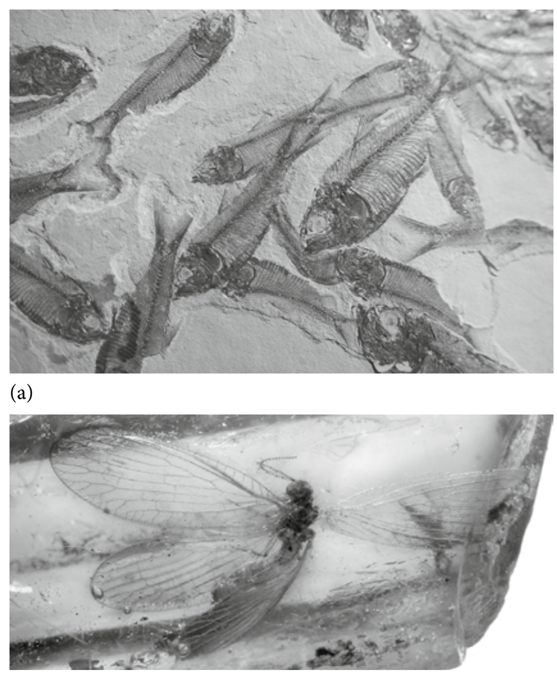
These are all questions about paleobiology and, surprisingly, a great deal can be inferred about these questions. **Fossils**, the remains of any ancient organism, may look like random pieces of rock in the shape of bones, leaves, or shells, but they can reveal their secrets to the properly trained scientist. **Paleontology**, the study of the life of the past, is like a crime scene investigation – there are clues here and there, and the **paleontologist** can use these clues to understand something about an ancient plant or animal, or a whole **fauna** or **flora** – the animals or plants that lived together in one place at one time.

In this chapter we will explore the methods of paleontology, starting with the debate about how dinosaurs are portrayed in films, and then look more widely at the other kinds of inferences that may be made from fossils. We will also consider how you could construct a career for yourself as a paleontologist. But first, just what is paleontology for? Where does it sit in the ranks of modern science?

PALEONTOLOGY IN THE MODERN WORLD

A few decades ago, the main purpose of paleontology was to date rocks. Many paleontology textbooks justified the subject in terms of its utility and contribution to industry. Others simply said that fossils are beautiful, and people love to look at them and collect them (Figure 1.1). But there is more to paleontology than that. We identify six reasons why paleontology is important:

1 *Origins*. People want to know about origins – where life came from, where humans came from, and where the Earth



(a)

(b)

Figure 1.1 People love to collect fossils. Many professional paleontologists go into the field because of the buzz of finding something beautiful that comes from a plant or animal that died millions of years ago. Fossils such as these tiny fishes from the Eocene of Wyoming (a), may amaze us by their abundance, or like the lacewing fly in amber (b), by the exquisite detail of their preservation. Source: Courtesy of Sten Lennart Jakobsen.

and universe came from. These have been questions in philosophy, religion, and science for thousands of years and paleontologists play a key role in revealing their answers. Despite the spectacular progress in paleontology, the earth sciences, and astronomy over the last two centuries, many people with fundamentalist religious beliefs deny all natural explanations of origins – these debates are hugely important, and paleontologists contribute vital information to the discussion.

2 *Curiosity about different worlds*. Science fiction and fantasy novels challenge and excite us with worlds that are different from our own. Another way to explore alien worlds is to study paleontology – the plants and animals that existed in the past were quite unlike any modern organism (see Chapters 10–19). Just imagine a world with land animals 10 times the size of elephants, a world with higher oxygen levels than today and dragonflies the size of seagulls, a world with only microbes, or a time when two or three different species of humans lived side by side in Africa!

3 *Climate and biodiversity change*. Thinking people, and now even politicians, are concerned about climate change and the future of life on Earth. Much can be learned by studying the modern world, but key evidence about likely future changes over hundreds or thousands of years comes from studies of what has happened in the past (see Chapter 8). For example, 252 million years ago, the Earth went through a phase of substantial global warming, acid rain, and declining oxygen levels, which resulted in 95% of species dying out (see Chapter 8); might this be relevant to current debates about the future?

4 *The shape of evolution*. The **tree of life** is a powerful and all-embracing concept (see Chapter 7). This is the idea that all species – living and extinct – are related to each other, and their relationships may be represented by a great branching tree that links us all back to a single species somewhere deep in the Precambrian (see Chapter 9). Biologists want to know how many species there are on the Earth today, how life became so diverse, and the nature and rates of diversifications and extinctions (see Chapter 8; Sections "The Diversification of Life" and "The "Big Five" Mass Extinction Events"). It is impossible to understand these great patterns of evolution from studies of living organisms alone.

5 *Extinction*. Fossils show us that extinction is a normal phenomenon: no species lasts forever. Without the fossil record, we might imagine that extinctions have been caused mainly by human interventions, and we would have no concept of mass extinctions, times when vast numbers of species die out (see Chapter 8; Section "Mass Extinctions").

6 *Dating rocks*. **Biostratigraphy**, the use of fossils in dating rocks (see Chapter 2), is a powerful tool for understanding deep time, and it is widely used in scientific studies, as well as by commercial geologists who seek oil and mineral deposits. Radioisotopic dating provides precise dates in millions of years for rock samples (radiocarbon dating is used by archaeologists because it spans back only thousands of years), but this technological approach only works with certain kinds of rocks. Fossils are very much at the core of modern stratigraphy, both for economic and industrial applications and as the basis of our understanding of Earth's history at local and global scales.

Paleontologists can come to the subject early, as children, or later through courses in geology or biology at university. Many students ask how they might find a career as a paleontologist, and the best way to weigh your options may be to look at some young people who have done just that (see Box 1.1).

PALEONTOLOGY AS A SCIENCE

What is science?

Imagine you are traveling by plane and your neighbor sees you reading an article about the life of the ice ages in a recent issue of *National Geographic*. She asks you how anyone can know about those mammoths and sabertooth cats, and how they could make those color paintings; surely they are just pieces of art, and not science at all? How would you answer?

Box 1.1 Careers in paleontology

Here are four people who have made careers in paleontology. The usual route is to first obtain a Bachelor's degree in Geology, Earth sciences, or Biology, after which pursuing a specialist Master's program in Paleontology, Museum studies, Micropaleontology, or some other specialism, and often a PhD (doctorate). Research posts in universities, colleges, and museums usually require a PhD, and the same is often true for jobs in industry, but paleontologists in the oil industry may have a Bachelor's degree and a specialist Master's, focusing especially on the use of microfossils in stratigraphy.

Dr. Erin Saupe (Figure 1.2a), Assistant Professor of Palaeobiology at the University of Oxford and former postdoc at the Yale Institute for Biospheric Studies, works on the ecological and evolutionary controls on species' environmental tolerances, the causes and consequences of both background and mass extinction, and the mechanisms and drivers responsible for diversification (see also Box 8.6). Here, she explains how she fell in love with paleontology and gives her advice for undergraduates pursuing a career in the field: "I fell head over heels for paleontology after taking a historical geology class as an undergraduate student. Although I had always been enamored with dinosaurs, entirely new creatures and ancient settings were revealed to me during this course, and I began to understand science as a process. I love that paleobiologists are similar to detectives: they work to piece together the history of life on Earth and the processes dictating that history. I care very deeply about sustaining life on Earth, and I use what happened to species in the past as a way to better understand and predict what might happen to them under present-day and future environmental changes. If you're interested in paleontology as an undergraduate, I would take as many courses in biology and geology as possible. Paleobiology is becoming increasingly quantitative, and future success in the field will be predicated – in part – on mathematical skills. For example, take as many modeling, programming, statistics, and calculus courses as you can stand (statistics being especially important). Seek out opportunities for independent research (e.g. with faculty at universities, museum settings, or national parks): the more experience you have with research early on, the more successful you will be in the future. Graduate school is increasingly competitive, and having research experience gives you an important leg up in the applicant pool."

Dr. Melanie Hopkins (Figure 1.2b), Associate Curator of Invertebrate Paleontology at the American Museum of Natural History, New York, works on the evolution of body shapes in trilobites (see also Box 6.3) and other arthropods. Here she comments on what paleontology means to her and recommends interested undergraduates to become fluent in as many scientific disciplines as possible: "I collected rocks and shells and sand as a child, and I loved learning about photosynthesis in high school. However, my first influential exposure to geology was not until college when I took some introductory courses on a whim, notably a course on coastal processes. And it was later still, when working at the U.S. Geological Survey, that I started reading about the early evolution of animals and thinking seriously about the coevolution of the Earth and life. The awesome and humbling time scales that had captivated me as a geology student were relevant for evolutionary biology! But studying paleobiology has also informed my everyday life, my opinions on current events, public policy, conservation, and my thinking about what life is and what it means to be human. Paleobiology is an integrative field of study, and this makes it a more demanding pursuit than commonly perceived. To be a professional, it is not enough to be able to identify fossils. The aspiring paleobiologist must gain some expertise in biology (such as evolutionary theory, quantitative genetics, systematics, phylogenetics, evo-devo, biochemistry, biogeography, ecology), geology (such as sedimentology, stratigraphy, Earth history, isotope analysis, geochemistry, taphonomy), statistics and various applied mathematics (such as linear algebra, time series analysis, model selection), and/or computer science (or at least an ability to code in something like R, C++, or Python)."

Dr. Maria McNamara (Figure 1.2c), Senior Lecturer at the University of Cork, Ireland, and formerly a postdoc at Yale and Bristol, UK, works on taphonomy of fossils, especially the chemistry

Figure 1.2 Paleontologists who are beginning their professional careers: (a) Dr. Erin Saupe discovers a fossil; (b) Dr. Melanie Hopkins collects trilobites bed-by-bed; (c) Dr. Maria McNamara takes notes as she logs a sedimentary section; and (d) Dr. Phoebe Cohen is happy to have found a near-perfect Precambrian stromatolite. Source: Images courtesy of their subjects.

of exceptional preservation of color in fossil insects and vertebrates (see also Box 5.1). She describes her sense of wonder and excitement in thinking about the life of the past: "The natural world has been my passion for as long as I can remember. As a child I pored over books about natural history. My real inspiration was my grandmother, and she sent us out into the fields with instructions to find different types of grasshopper or snail or some such. I still remember the satisfaction of identifying our precious finds using her wonderful library of reference books. My grandmother also brought us hunting for fossils in the local slate quarries, and this made me determined to pursue geology as a career. To me palaeobiology is one of the most exciting scientific fields today because it's a melting pot of evolutionary biology, classical palaeontology, sedimentology, geochemistry, geology, and more. My research is driven by a couple of fundamental questions: How are fossils preserved? How can fossils help us understand evolutionary trends and processes through deep

Continued

time? To younger students considering palaeontology as a career, my advice would be to study hard, gain relevant experience in a research group or museum, and read widely – this will broaden your knowledge base and understanding, and will help you identify what excites you most. Being a paleontologist often involves long hours in the lab, in the field, or writing papers, but when you're passionate about the subject, the hours fly by. It's hard sometimes to strike a balance between work and family life, but having young children has had a very definite positive impact on my work – I'm more focused and efficient now."

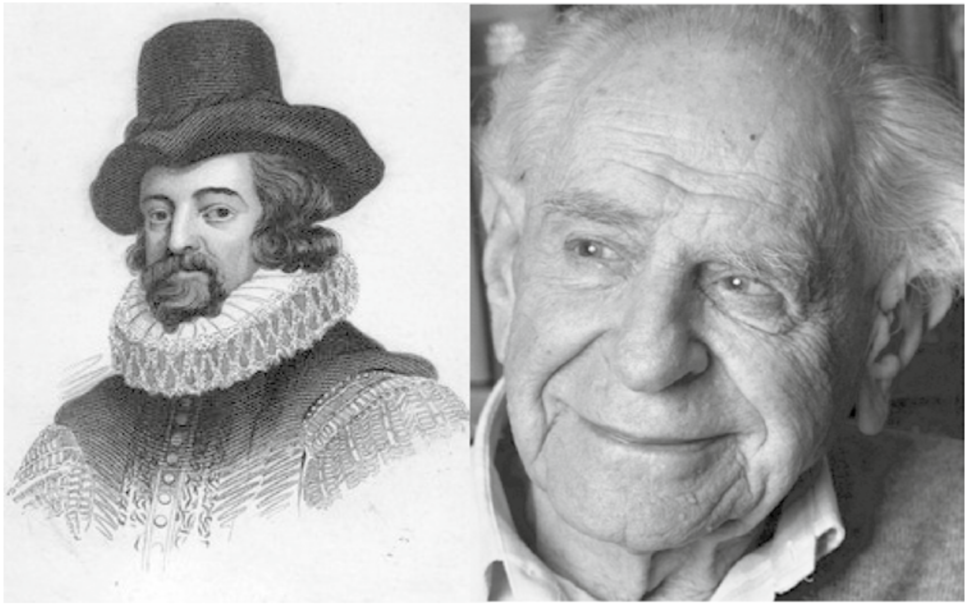
Dr. Phoebe Cohen (Figure 1.2d), Associate Professor of Geosciences at Williams College, Williamstown, Massachusetts, works on microscopic fossils from the Precambrian, exploring early life on Earth, and contributing to astrobiology as well as paleobiology. She describes why she finds the origin and early history of life so awesome: "I was inspired by going to the Harvard Museum of Natural History with my parents as a child, my 7th-grade Earth science teaching, and reading lots of National Geographic magazines. My driving inspiration is a desire to understand how the world got to be the way it is today, and what events have shaped life on earth through time. I love paleobiology because it's interdisciplinary and I am constantly learning and pushing myself as a scientist. I feel very fortunate that my profession lets me incorporate different ways of thinking about the world around me. I'm interested in understanding how earth and life have co-evolved through time. This is a big question, so I focus mainly on one time period, the Neoproterozoic, which is the time period leading up to the radiation of animals in the Cambrian Period. I'm really interested in how eukaryotes evolved in the Neoproterozoic (see also Box 9.3), what that can tell us more broadly about how life responds to environmental change, and how environments are themselves influenced by life over time. I find these questions endlessly interesting, which means I picked a good area to study! To me, the three keys to success are enthusiasm, curiosity, and persistence. If you don't truly feel enthusiasm for what you do, have curiosity about what you are working on, and persist at your work, it's hard to make it through the tough, boring, stressful times (and there will be plenty of those!)."

Science is supposed to be about reality, about hard facts, calculations, and proof. It is obvious that you cannot take a time machine back 20 000 years and see the mammoths and sabertooths for yourself; so how can we ever claim that there is a scientific method in paleontological reconstruction?

There are two ways to answer this: the first is obvious, but a bit of a detour, and the second gets to the core of the question. So, to justify those colorful paintings of extinct mammals, your first answer could be: "Well, we dig up all these amazing skeletons and other fossils that you see in museums around the world – surely it would be pretty sterile just to stop and not try to answer questions about the animal itself – how big was it, what were its nearest living relatives, when did it live?" From the earliest days, people have always asked questions about where we come from, about origins. They have also asked about the stars, about how babies are made, about what lies at the end of the rainbow. So, the first answer is to say that we are driven by our insatiable curiosity and our sense of wonder to try to find out about the world, even if we do not always have the best tools for the job.

The second answer is to consider the nature of **science**. Is science only about certainty, about proving things? In mathematics, and many areas of physics, this might be true. You can attempt to measure the distance to the moon, to calculate the value of pi, or to derive a set of equations that explain the moon's influence on the Earth's tides. Generation by generation, these measurements and proofs are tested and improved. But this approach does not work for most of the natural sciences. Here, there have been two main approaches: induction and deduction.

Sir Francis Bacon (1561–1626), a famous English lawyer, politician, and scientist (Figure 1.3a), established the methods of **induction** in science. He argued that it was only through the patient accumulation of accurate observations of natural phenomena that a problem could be solved. The enquirer might hope to see common patterns among the observations, and these common patterns would point to an explanation, or law



(a) (b)

Figure 1.3 Important figures in the history of science: (a) Sir Francis Bacon (1561–1626), who established the methods of induction in science; and (b) Karl Popper (1902–1994), who explained that scientists adopt the hypothetico-deductive method.

of nature. Bacon famously met his death perhaps as a result of his restless curiosity about everything; he was traveling in the winter of 1626, and was experimenting with the use of snow and ice to preserve meat. He bought a chicken, and got out of his coach to gather snow, which he stuffed inside the bird; he contracted pneumonia and died soon after. The chicken, on the other hand, was fresh to eat a week later, so proving his case.

The other approach to understanding the natural world is a form of **deduction**, where a series of observations point to an inevitable outcome. This is a part of classical logic dating back to Aristotle (384–322 BCE) and other ancient Greek philosophers. The standard logical form goes like this:

All men are mortal.
Socrates is a man.
Therefore Socrates is mortal.

Deduction is the core approach in mathematics and in detective work, of course. How does it work in science?

Karl Popper (1902–1994) described the way that science works as the **hypothetico-deductive method**. Popper (Figure 1.3b) argued that in most of the natural sciences, proof is impossible. What scientists do is to set up **hypotheses**, statements about what may or may not be the case. An example of a hypothesis might be "*Smilodon*, the saber-toothed cat, was exclusively a meat eater." This can never be proved absolutely, but it could be refuted and therefore rejected. So what most natural scientists do is called **hypothesis testing**; they seek to **refute**, or disprove, hypotheses rather than to prove them. Paleontologists have made many observations about *Smilodon* that tend to confirm, or **corroborate**, the hypothesis: it had long sharp teeth, bones have been found with bite marks made by those teeth, fossilized *Smilodon* turds contain bones of other mammals, and so on. But it would take just one discovery of a *Smilodon* skeleton with leaves in its stomach area, or in its excrement, to disprove the hypothesis that this animal fed exclusively on meat.

Science is of course much more complex than this. Scientists are human, and they are subject to all kinds of influences and prejudices, just like anyone else. Scientists follow trends, they are slow to accept new ideas, and they may prefer one interpretation over another because of some political or sociological belief. Thomas Kuhn (1922–1996) argued that science shuttles between so-called times of normal science and times of scientific revolution. Scientific revolutions, or **paradigm shifts**, are when a whole new idea invades an area of science. At first people may be reluctant to accept the new idea, and they fight against it. Then some scientists speak up and support it, and then everyone does. This is summarized by the old truism – when faced with a new idea most people at first reject it, then they begin to accept it, and then they say they knew it all along.

A good example of a paradigm shift in paleontology was triggered by the paper of Luis Alvarez et al. (1980) in which they presented the hypothesis that the Earth had been hit by a meteorite 66 million years ago, and this impact caused the extinction of the dinosaurs and other groups. It took 10 years or more for the idea to become widely accepted as the evidence built up (see Chapter 8; Section "The Cretaceous-Paleogene event"). As another example, current attempts by religious fundamentalists to force their view of "intelligent design" into science will likely fail because they do not test evidence rigorously, and paradigm shifts only happen when the weight of evidence for the new theory overwhelms the evidence for the previous view (see Chapter 7; Section "Evolution and the Fossil Record").

So science is curiosity about how the world works. It would be foolish to exclude any area of knowledge from science, or to say that one area of science is "more scientific" than another. There is mathematics and there is natural science. The key point is that there can be no proof in natural science, only hypothesis testing. But where do the hypotheses come from? Surely they are entirely speculative?

Speculation, hypotheses, and testing

There are facts and speculations. "The fossil is 6 centimeters long" is a fact; "it is a leaf of an ancient fern" is a speculation. But perhaps the word "speculation" is the problem, because it sounds as if the paleontologist simply sits back with a glass of brandy and a cigar and lets his or her mind wander idly. But speculation is constrained within the hypothetico-deductive framework.

This brings us to the issue of hypotheses and where they come from. Surely there are unknown millions of hypotheses that could be presented about, say, the trilobites? Here are a few: "trilobites were made of cheese;" "trilobites ate early humans;" "trilobites still survive in Alabama;" "trilobites came from the moon." These are not useful hypotheses, however, and would never be set down on paper. Some can be refuted without further consideration – humans and trilobites did not live at the same time, and no one in Alabama has ever seen a living trilobite. Admittedly, one discovery could refute both of these hypotheses. Trilobites were almost certainly not made from cheese as their fossils show cuticles and other tissues and structures seen in living crabs and insects. "Trilobites came from the moon" is probably an untestable (as well as wild) hypothesis.

So, hypotheses are narrowed down quickly to those that fit the framework of current observations and that may be tested. A useful hypothesis about trilobites might be: "trilobites walked by making leg movements like modern millipedes." This can be tested by studying ancient tracks made by trilobites, by examining the arrangement of their legs in fossils, by studies of how their modern relatives walk, and by constructing functional digital computer models. So, **hypotheses should be sensible and testable**. This still sounds like speculation, however. Are other natural sciences the same?

Of course they are. The natural sciences operate by means of hypothesis testing. Which geologist can put his finger on the atomic structure of a diamond, the core–mantle boundary, or a magma chamber? Can we prove with 100% certainty that mammoths walked through Manhattan and London, that ice sheets once covered most of Canada and northern Europe, or that there was a meteorite impact on the Earth 66 million years ago? Likewise, can a chemist show us an electron, can an astronomer confirm the composition of stars that have been studied by spectroscopy, can a physicist show us a quantum of energy, and can a biochemist show us the double helix structure of DNA?

So, the word "speculation" can mislead; perhaps "**informed deduction**" would be a better way of describing what most scientists do. Reconstructing the bodily appearance and behavior of an extinct animal is identical to any other normal activity in science, such as reconstructing the atmosphere of

Saturn or the structure of DNA. The sequence of observations and conjectures that stand between the bones of *Brachiosaurus* lying in the ground and its reconstructed moving image in a movie is identical to the sequence of observations and conjectures that lie between biochemical and crystallographic observations on chromosomes and the creation of the model of the structure of DNA. Both hypotheses (the image of *Brachiosaurus* or the double helix) may be wrong, but in both cases the models reflect the best fit of the data to the facts. The critic has to provide evidence to refute the hypothesis, and, most importantly, present a replacement hypothesis that fits the data better. Refutation and skepticism are the gatekeepers of science – ludicrous hypotheses are quickly weeded out, and the remaining hypotheses have survived criticism (so far).

Fact and fantasy – where to draw the line?

As in any science, there are levels of certainty in paleontology. The fossil skeletons show the shape and size of a dinosaur, the rocks show where and when it lived, and associated fossils show other plants and animals of the time. These can be termed **facts**. Should a paleontologist go further? It might be useful to think about a sequence of deductive steps used by a paleontologist to go from bones in the ground to a walking, moving reconstruction of an ancient organism. And this sequence roughly matches a sequence of decreasing certainty, in three steps.

The first step is to **reconstruct** the skeleton – to put it back together. Most paleontologists would accept that this is a valid thing to do, and there is very little guesswork in identifying the bones and putting them together in a realistic pose. The next step is to reconstruct the muscles. This step might seem highly speculative, but then all living vertebrates – frogs, lizards, crocodiles, birds, and mammals – have pretty much the same sorts of muscles, so it is likely dinosaurs did too. Also, muscles leave scars on the bones that show where they attached. So, the muscles go on to the skeleton – either on a model, with muscles made from clay, or on a digital model within a computer – and these provide the body shape. Other soft tissues, such as the heart, liver, eyeballs, tongue, and so on are rarely preserved (though surprisingly such tissues are sometimes exceptionally preserved; see Chapter 5; Section "Exceptional preservation"), but again their size and positions are predictable from modern relatives. Even the skin is not entirely guesswork: some mummified dinosaur specimens show the patterns of scales set in the skin.

The second step is to work out the basic biology of the ancient beast. The teeth hint at what the animal ate, and the jaw shape shows how it fed. The limb bones show how the dinosaurs moved. You can manipulate the joints and calculate the movements, stresses, and strains of the limbs. With care, it is possible to work out the pattern of locomotion in great detail. All the images of walking, running, swimming, and flying shown in TV documentaries are generally based on careful calculation and modeling, and comparison with living animals. The movements of the jaws and limbs have to obey the laws of physics (gravity, lever mechanics, and so on). So these broad-scale indications of paleobiology and biomechanics are defensible and realistic.

The third level of certainty includes the colors and patterns, the breeding habits, the noises. However, even these, although usually unsupported by fossil data, are not fantasy. Paleontologists, like any people with common sense, base their speculations here on comparisons with living animals. How did dinosaurs reproduce? There are many examples of dinosaur nests with eggs, so paleontologists know how many eggs were laid and how they were arranged for some species. Some suggested that the parents cared for their young, while others said this was nonsense. But the modern relatives of dinosaurs – birds and crocodilians – show different levels of parental care. Then, in 1993, a specimen of the flesh-eating dinosaur *Oviraptor* was found in Mongolia sitting over a nest of *Oviraptor* eggs – perhaps this was a chance association, but it seems most likely that it really was a parent brooding its eggs. But what about color? Surely there can never be any evidence about the original color of a dinosaur, or any extinct plant or animal for that matter? Well, a discovery in 2010 showed concrete evidence of dinosaur color, and electrified the world of paleontology (see Box 1.2).

So, when you see a walking, grunting dinosaur, or a leggy trilobite, trotting across

Box 1.2 Telling the color of a dinosaur

How quickly can viewpoints change! In discussing paleobiology, some things about ancient life might seem impossible to reconstruct. However, in 2010 two teams independently claimed to have reconstructed the original color and color patterns of a dinosaur in papers published in the world's leading scientific journals, first in *Nature* and then in *Science*. In the first paper, the small theropod dinosaur *Sinosauropteryx* was shown to have been all-over ginger in color, and with a ginger and white striped tail. In the second paper, the small theropod dinosaur *Anchiornis* was shown to have carried black and white stripes over its body, and to have had a reddish crest and speckled red and

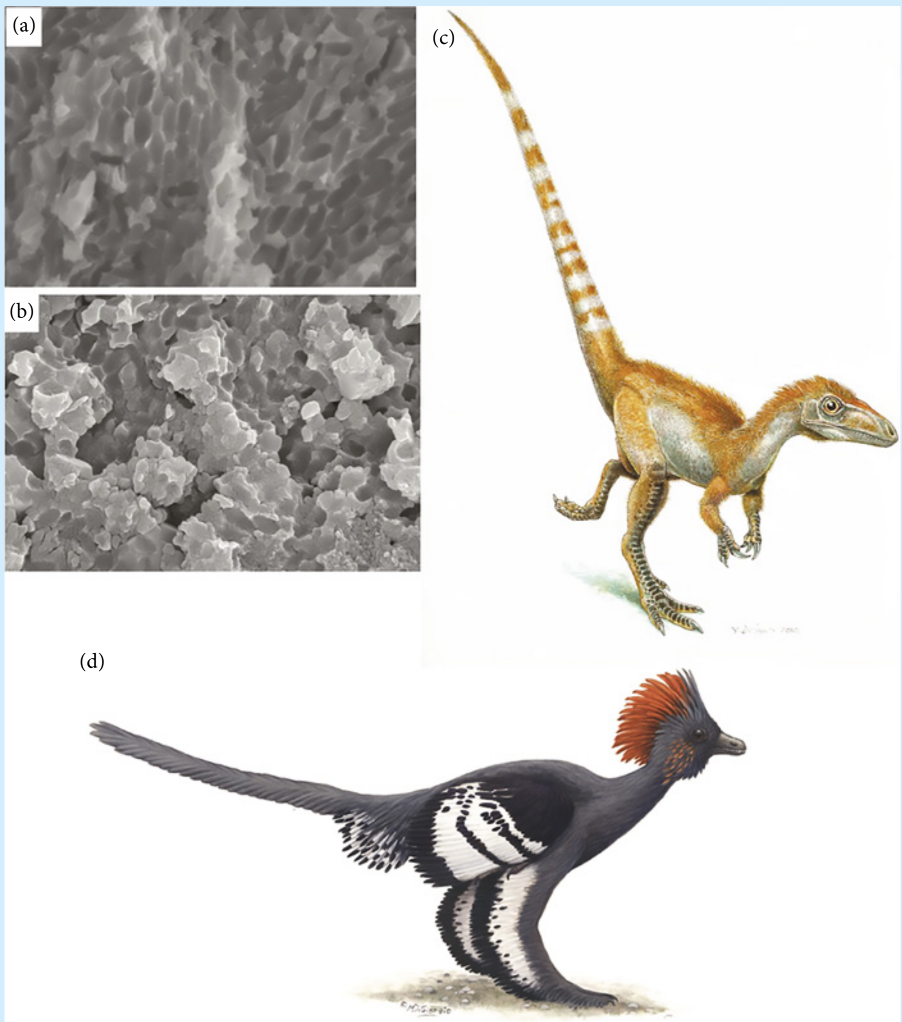


Figure 1.4 The colors of dinosaur feathers: (a, b) scanning electron microscope photographs of sausage-shaped eumelanosomes, indicating black, gray, or brown original colors (a), and of spherical phaeomelanosomes, indicating ginger colors (b); (c) reconstruction of *Sinosauropteryx*, showing the ginger and white striped tail; (d) reconstruction of *Anchiornis*, showing black, gray, ginger, and white color stripes and patches. See Color plate 9.1. Source: (a, b) Zhang et al. (2010). Reproduced with permission from Nature Publishing Group. (c) J. Robins (artist), Bath, UK. Reproduced with permission. (d) M. DiGiorgio, Madison, CT, USA. Reproduced with permission.

gray cheeks. Many paleontologists doubted these results, and some still deny them, but the evidence was clear.

The story began in 2008, when Yale graduate student Jakob Vinther looked again at what had been identified as bacteria within a fossil feather from Brazil. At high magnification under the scanning electron microscope, the tiny, sausage-shaped structures looked just like coccoid bacteria, but Vinther noticed they were only seen in dark-colored stripes in the feather, not in the pale-colored stripes. He made a lateral jump and realized these were not bacteria but rather melanosomes, crowded within originally black bands and absent in originally white bands. The fossil feather showed only dark and light colors, and these could well have been any color in life. However, if the minute organelles were melanosomes, then he had direct evidence of original color.

Melanosomes are abundant in the feathers of birds and the hair of mammals. Melanosomes contain the pigment molecule melanin, which occurs in two variants. Eumelanin, the common variant, gives gray, brown, and black colors, while less frequent phaeomelanin gives ginger colors. These two organic pigments provide all the colors of mammalian, including human, hair, whereas birds use melanin commonly for feather color, but add some dietary pigments such as carotenes and porphyrins, for yellows, red, purples, and greens. Eumelanosomes are generally sausage-shaped organelles about 1 μm (= 1 millionth of a meter) in length (Figure 1.4a), phaeomelanosomes are generally spherical and half that size (Figure 1.4b).

So, in the 2010 papers, the team working on *Sinosauropteryx* identified only phaeomelanosomes in its fossilized feathers, and clear evidence for presence-absence in stripes along the tail (Figure 1.4c), and the team working on *Anchiornis* found both melanosome types in feathers from different regions of its body (Figure 1.4d).

These papers showed two things: that color in dinosaurs could be determined (only in feathered dinosaurs), and that display might have been important in these early forms, just as in birds today, and that perhaps scientists should never say something is impossible – as Peter Medawar, renowned medical researcher, said in the 1950s, "science is the art of the possible."

Read more about these discoveries in Zhang et al. (2010) and Li et al. (2010), and at https://dinocolour.blogs.bristol.ac.uk. The latest is that pterosaurs, the flying reptiles, also had melanosomes in their fluff, and indeed it seems likely that their "fluff" is the same as bird-dinosaur feathers, meaning feathers and feather color originated much earlier than anyone had thought before (Yang et al. 2019).

your TV screen, or featured in magazine artwork, is it just fantasy and guesswork? Perhaps you can now tell your traveling companion that it is a reasonable interpretation, probably based on a great deal of background work. The body shape should be reasonably correct, the movements of jaws and limbs are based on structural experiments with the fossil skeletons and as realistic as they can be, and the colors, noises, and behaviors may have more evidence behind them than you would imagine at first.

Paleontology and the history of images

Debates about science and testing in paleontology have had a long history. This can be seen in the history of images of ancient life: at first, paleontologists just drew the fossils as they saw them. Then they tried to show what the perfect fossil looked like, repairing cracks and damage to fossil shells, or showing a skeleton in a natural pose. For many in the 1820s, this was enough; anything more would not be scientific.

However, some paleontologists dared to show the life of the past as they thought it looked. After all, this is surely one of the aims of paleontology? And if paleontologists do not direct the artistic renditions, who will? The first line drawings of reconstructed extinct animals and plants appeared in the 1820s (Figure 1.5). By 1850, some paleontologists were working with artists to produce life-like paintings of scenes of the past, and even three-dimensional models for museums. The growth of museums, and improvements in printing processes, meant that by 1900 it was commonplace to see color paintings of scenes from ancient times, rendered by skillful artists and supervised by reputable paleontologists. Moving dino-

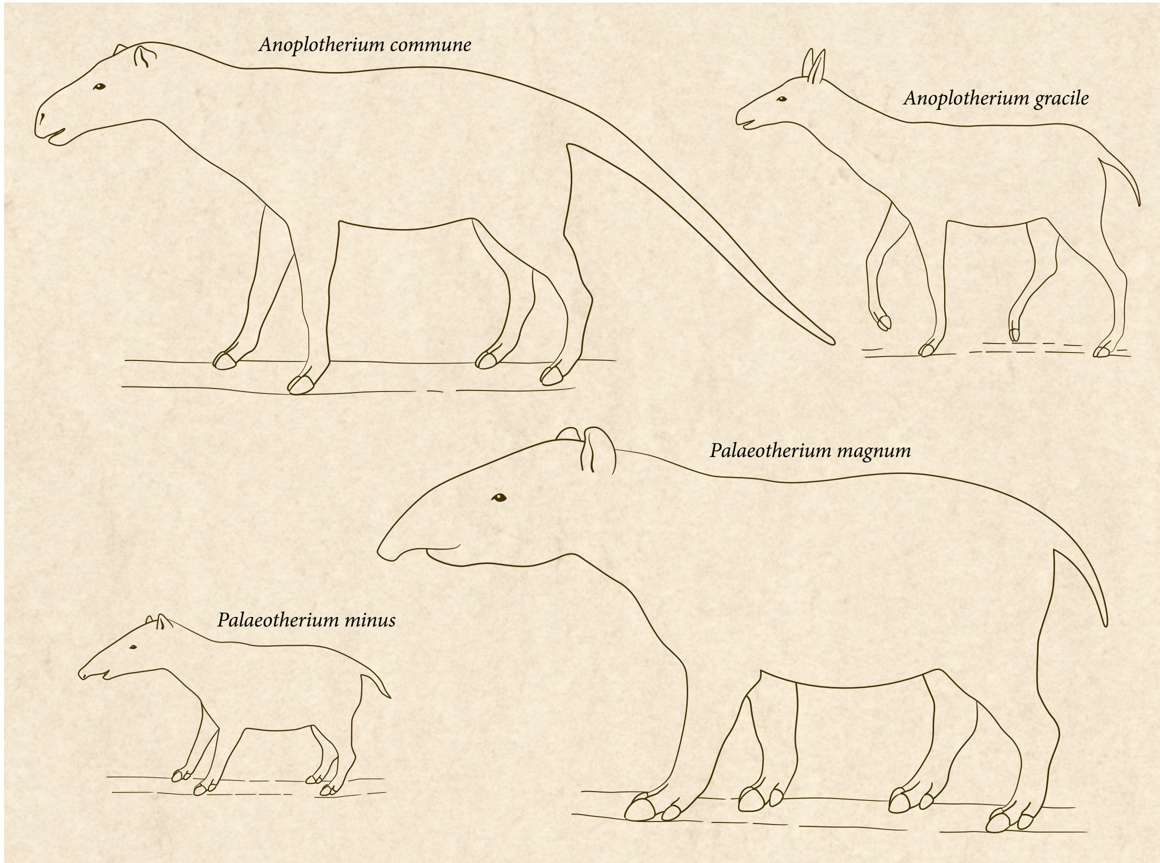


Figure 1.5 Some of the earliest reconstructions of fossil mammals. These outline sketches were drawn by C. L. Laurillard in the 1820s and 1830s, under the direction of Georges Cuvier. The image shows two species each of *Anoplotherium* and *Palaeotherium*, based on specimens Cuvier had reconstructed from the Tertiary deposits of the Paris Basin. Source: Modified from Cuvier 1834–1836.

saurs, of course, have had a long history in Hollywood movies through the twentieth century, but the world had to wait until the technology allowed more realistic computer-generated renditions in the 1990s, first in *Jurassic Park* (1993), and then in *Walking with Dinosaurs* (1999), *Jurassic World* (2015), and hundreds of films and documentaries each year (Box 1.3). Paleontologists often complain about the Hollywood dinosaurs, but often they are worried about details, and in fact their websites and museums may very well use the same digital technologies to produce physical models and computer-generated images that breathe life into fossil organisms.

The slow evolution of reconstructions of ancient life over the centuries reflects the growth of paleontology as a discipline. How did the first scientists understand fossils?

STEPS TO UNDERSTANDING

Earliest fossil finds

Fossils are very common in certain kinds of rocks, and they are often attractive and beautiful objects. It is probable that people picked up fossils long ago, and perhaps even wondered why shells of sea creatures are now found high in the mountains, or how a perfectly preserved fish specimen came to lie buried deep within layers of rock. Prehistoric peoples picked up fossils and used them as ornaments, presumably with little understanding of their meaning.

Some early speculations about fossils by classical authors seem now very sensible to modern observers. Early Greeks such as Xenophanes (576–480 BCE) and Herodotus (484–426 BCE) recognized that some fossils were marine organisms, and that these provided evidence for earlier positions of the

Box 1.3 Bringing dinosaurs to life

Everyone's image of dinosaurs and ancient life changed in 1993. Steven Spielberg's film *Jurassic Park* was the first to use the new technique of computer-generated imagery (CGI) to produce realistic animations. Older dinosaur films had used clay models or lizards with cardboard crests stuck on their backs. These looked pretty terrible and could never be taken seriously by paleontologists. Up to 1993, dinosaurs had been reconstructed seriously only as two-dimensional paintings and three dimensional museum models. CGI made those superlative color images move.

Following the huge success of *Jurassic Park*, Tim Haines at the BBC in London decided to try to use the new CGI techniques to produce a documentary series about dinosaurs. Year by year, desktop computers were becoming more powerful, and the CGI software was becoming more sophisticated. What had once cost millions of dollars now cost only thousands. This resulted in the series *Walking with Dinosaurs*, first shown in 1999 and 2000, a classic BBC production that is still a benchmark of collaboration between paleontologists, computer modelers, and filmmakers.

The documentary producers chose six or seven key beasts per episode. Each of these animals was studied in depth by consultant paleontologists and artists, and a carefully measured clay model (maquette) was made. This was the basis for the animation. The maquette was laser scanned, and turned into a virtual "stick model" that could be moved in the computer to simulate running, walking, jumping, and other actions.

While the models were being developed, BBC film crews went round the world to film the background scenery. Places were chosen that had the right topography, climate, and plants. Where ancient mammals splashed through water, or grabbed a branch, the action (splashing, movement of the branch) had to be filmed. Then the animated beasts were married with the scenery by the CGI company. This is hard to do, because shadowing and reflections had to be added, so the animals interacted with the backgrounds. If they run through a forest, they have to disappear behind trees and bushes, and their muscles have to move beneath their skin (Figure 1.6); all this can be semiautomated through the CGI software.

In a recent production, *Attenborough and the Giant Dinosaur* (BBC, 2015–2016), the whole process, from bones in the ground to a fully skin-covered and animated titanosaur, was shown. David Attenborough walked round the reconstructed skeleton of one of the largest ever dinosaurs,

Figure 1.6 The world's largest dinosaur, a titanosaur from Argentina, as portrayed in "David Attenborough and the Giant Dinosaur," a film aired in 2015 and 2016.
Source: Courtesy of Robin Cox, BBC Natural History Unit.

Continued

built in an aircraft hangar, and the CGI team used high-resolution 3D scans of the fossil bones to create a virtual skeleton, which was articulated correctly with the help of paleontologists and comparative anatomists. This model was then used to place the internal organs, such as the heart and lungs, with the help of a comparative anatomist. The bones were then clothed with muscle and covered with skin, helping to create a moving "live" dinosaur. Such details and effects are key to the success of dinosaur movies and documentaries, but would be nothing without the close collaboration between the documentary producers, CGI experts and anatomists, and paleontologists.

CGI effects are commonplace now in films, advertising, and educational applications. From a start in about 1990, the industry now employs thousands of people, and many of them work full-time on making paleontological reconstructions for leading TV companies and museums.

oceans. Other classical and medieval authors, however, had a different view.

Fossils as magical stones

In Roman and medieval times, fossils were often interpreted as mystical or magical objects. Fossil sharks' teeth were known as *glossopetrae* ("tongue stones"), in reference to their supposed resemblance to tongues, and many people believed they were the petrified tongues of snakes. This interpretation led to the belief that the glossopetrae could be used as protection against snakebites and other poisons. The teeth were worn as amulets to ward off danger, and they were even dipped into drinks in order to neutralize any poison that might have been placed there.

Most fossils were recognized as *looking like* the remains of plants or animals, but they were said to have been produced by a "plastic force" (*vis plastica*) that operated within the Earth. Numerous authors in the sixteenth and seventeenth centuries wrote books presenting this interpretation. For example, the Englishman Robert Plot (1640–1696) argued that ammonites (see Chapter 14) were formed "by two salts shooting different ways, which by thwarting one another make a helical figure." These interpretations seem ridiculous now, but there was a serious problem in explaining how such specimens came to lie far from the sea, why they were often different from living animals, and why they were made of unusual minerals and embedded deep within solid rock.

The idea of plastic forces had been overthrown largely by the 1720s, but some extraordinary events in Wurzburg, Germany, contributed to its downfall at the time. Johann Beringer (1667–1740), a professor at the university, began to describe and illustrate "fossil" specimens brought to him by collectors from the surrounding area. These collectors, however, had been paid by an academic rival to manufacture "fossils" by carving the soft limestone into the outlines of shells, flowers, butterflies, and birds (Figure 1.7). There was even a slab with a pair of mating frogs, and others with astrologic symbols and Hebrew letters. Beringer resisted evidence that the specimens were forgeries, and wrote as much in his book, the *Lithographiae Wirceburgensis* (1726). He only realized the awful truth soon after publication.

Fossils as fossils

The debate about plastic forces was terminated abruptly by the debacle of Beringer's figured stones, but it had really been resolved rather earlier. Leonardo da Vinci (1452–1519), a brilliant scientist and inventor (as well as a great artist), used his observations of modern

Figure 1.7 Lying stones: two of the remarkable "fossils" described by Professor Beringer of Wurzburg in 1726: he believed these specimens represented real animals of ancient times that had crystallized into the rocks by the action of sunlight.