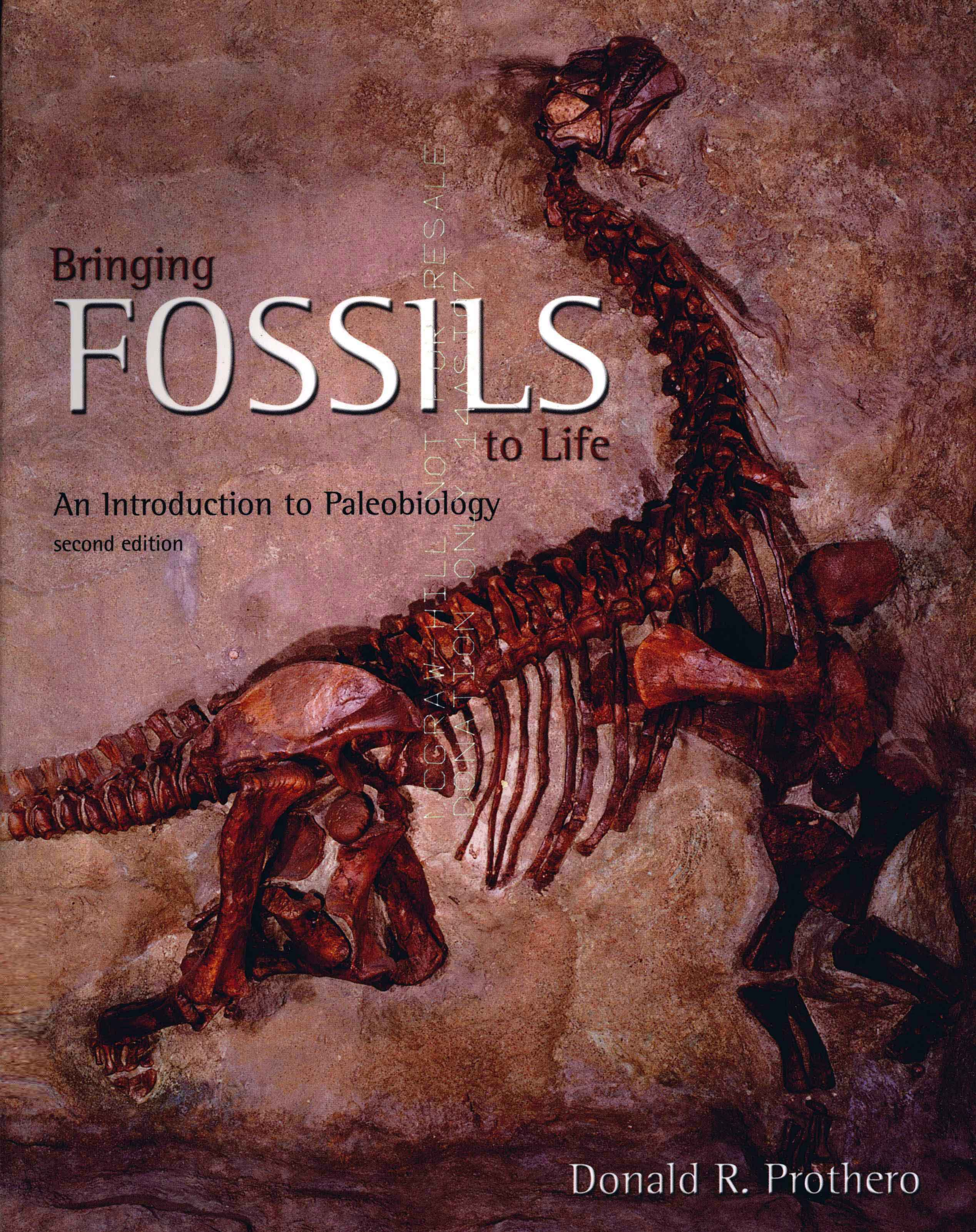

Bringing
FOSSILS
to Life

An Introduction to Paleobiology

second edition

Donald R. Prothero

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Donald R. Proth
Occidental College

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BRINGING FOSSILS TO LIFE: AN INTRODUCTION TO PALEOBIOLOGY
SECOND EDITION

This book is printed on recycled, acid-free paper containing 10% postconsumer waste.

4 5 6 7 8 9 0 QPD/QPD 0 9 8 7 6
ISBN 978-0-07-366170-4
MHID 0-07-366170-8

Publisher: *Margaret J. Kemp*
Sponsoring editor: *Thomas C. Lyon*
Developmental editor: *Lisa A. Leibold*
Executive marketing manager: *Lisa L. Gottschalk*
Senior project manager: *Mary E. Powers*
Lead production supervisor: *Sandy Ludovissy*
Coordinator of freelance design: *Michelle D. Whitaker*
Cover/interior designer: *Kaye Farmer*
Cover image: *Copyright, Carnegie Museum of Natural History*
Compositor: *Carlisle Communications, Ltd.*
Typeface: *10/12 Times Roman*
Printer: *Quebecor World Dubuque, IA*

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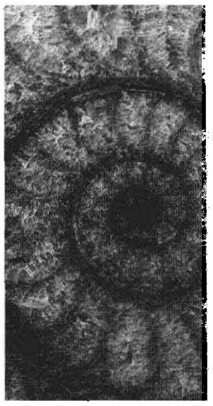
Library of Congress Cataloging-in-Publication Data

Prothero, Donald R.
Bringing fossils to life : an introduction to paleobiology / Donald R. Prothero.—2nd ed.
p. cm.
Includes bibliographical references and index.
ISBN 0–07–366170–8
1. Paleobiology. 2. Fossils. I. Title.

QE719.8.P76 2004
560—dc21 2002045239
CIP

www.mhhe.com



preface

Scientists in general might be excused for assuming that most geologists are paleontologists and most paleontologists have staked out a square mile as their life's work. A revamping of the geologist's image is badly needed.

Editorial, Nature, 1969

As well as being lumps of patterned stone, fossils are also historical documents. History per se has had a bit of bad press recently. . . . There is a tension between the documentation of history (famously referred to as "one bloody thing after another"), and the search for universal principles that are ahistoric and possibly timeless. After a period in the doldrums, the bearers of the historical tidings, the paleontologists, are making tentative movements toward the legendary High Table where, just visible through the clouds of incense (and rhetoric), the high priests of evolutionary theory smile benignly.

S. Conway Morris, "Early Metazoan radiations: what the fossil record can and cannot tell us," 1996

Paleontology is at a crossroads. For decades, introductory paleontology classes focused on the taxonomy and anatomy of the major phyla of fossil invertebrates. This traditional approach dates back at least a century, and has long given paleontology the bad reputation of drudgery. Paleontology was often equated with "stamp collecting." Paleontologists were caricatured as narrow specialists who were interested only in the trivial details of the names, ages, and shapes of their fossils.

In the 1970s, however, paleontology experienced a revolution. A new generation of "Young Turks" who earned their doctorates in the 1960s challenged the old obsession with trivial details and asked broader theoretical questions of the fossil record. How good is the fossil record, and what can (and can't) we read from it? What does the fossil record say about the tempo and mode of evolution? What do the patterns of mass extinction reveal about fragility of life on this planet? How do the movements of continents explain the distribution of fossils in time and space? How do we determine the relationships and evolutionary histories of extinct organisms? In the preface to the pioneering book *Models in Paleobiology* (1972), Tom Schopf described a revealing encounter with a young Ph.D. student who could not decide on his dissertation topic. Should he describe a collection of fossils his adviser had recently assembled? It never occurred to this student to ask *what problems he should be solving or what hypotheses he should be testing* using the fossil record.

This purely descriptive approach to paleontology became outmoded as the "Young Turks" changed the way we look at fossils. In 1972, Niles Eldredge and Stephen Jay Gould published their punctuated equilibrium model (in the Schopf book just mentioned), and that debate has been raging ever since. In 1975, Tom Schopf and Ralph Johnson founded *Paleobiology*, and it became the premier theoretical journal in the profession. In 1975, Steve Stanley first suggested the model of species selection, and evolutionary theory has since begun to rethink the issue of macroevolution. In 1980, the asteroid hypothesis for the extinction of dinosaurs was published, and the last 23 years have seen a tremendous bandwagon of interest in mass extinctions and their implications. For the last 20 years, the Paleontological Society meetings have featured papers of broad theoretical interest, with few talks that are purely local or descriptive in nature.

Ironically, this revolution in the practice of paleontology has barely worked its way into the teaching of paleontology. Most textbooks are highly detailed reviews of the anatomy and systematics of the major groups of fossil invertebrates, with only short chapters on theoretical topics. Having taught from several of these books, I have found that most of today's undergraduates are not prepared for this level of detail when they don't see the point in learning it all. Such an approach is more appropriate to advanced level or graduate courses in paleontology, after the student has become hooked on fossils and is motivated to master all those names. First, however, the instructor should give the student a sense of the excitement of the field, and explore the reasons why so many people find fossils fascinating, instead of killing their interest with excessive memorization. Other textbooks stress theoretical topics at a very high level but do not give the necessary background in the taxonomy and systematics so that the students can place the theory in context.

This book is an attempt to bridge the gap between purely theoretical paleobiology and purely descriptive invertebrate paleontology books. It is written for the general geology or biology majors who take paleontology for fun or as part of their requirements, not as an encyclopedia for professionals. The theoretical topics are covered in Part I, stressing the newer developments in paleobiology that should excite the student. Part II outlines the major features of the fossil record of vertebrates, invertebrates, and plants. Here, I have deliberately reduced the excessive memorization of taxa and anatomy to a bare minimum of terms that are essential in talking about each group. In my experience, most of this memorization is quickly forgotten unless there is a point to it, or a problem to be solved with it. Only students who plan to follow paleontology as a career should be expected to know the quantity of information that some other textbooks demand.

In both parts, I have tried to write at a level of detail appropriate to undergraduate geology majors with a previous course in historical geology, but with limited backgrounds in biology. Throughout the book, I have tried to capture a sense of the excitement of paleobiology and have tried to convey *why* we try to do what we do. Students today are very results-oriented, so in the back of my mind their persistent question "What's the point?" guided my writing. As I wrote, I kept in mind what 23 years of experience with some of the best undergraduates in the country (at Columbia, Vassar, Knox, and Occidental Colleges) has taught me about what students retain and what ideas excite them and keep their interest. If we can interest them at this level, then they will come back for more and be willing to learn more taxonomy and morphology. Then they will see how exciting paleobiology has become and possibly consider it to be their future as well.

Acknowledgments: I thank my McGraw-Hill editorial and marketing team, Marge Kemp, Lisa Leibold, Lisa Gottschalk, Fran Schreiber, and Beth Parkin for all their help. I thank Linda Ivany and Norman MacLeod for carefully critiquing Part I, and Marie-Pierre Aubry, Bill Ausich, Loren Babcock, John Barron, Bill Berggren, Dave Bottjer, Gilbert Brenner, Carl Brett, Sandy Carlson, Alan Cheetham, Mary Droser, Tony Ekdale, George Engelmann, James Firby, Tom Holtz, Jim Hopson, Conrad LaBandeira, Neil Landman, Dave Lazarus, Jere Lipps, Bill Orr, Kevin Padian, Roy Plotnick, John Pojeta Jr., J. Keith Rigby, Dave Schwimmer, William Siesser, Jim Sprinkle, George D. Stanley, Jr., and Karen Whittlesey for their helpful comments on various parts of the book. Many colleagues were very helpful in providing photographs or illustrations, and their contributions are acknowledged in the figure captions.

I thank T. Baumiller, R. Brame, B. Corliss, A. A. Ekdale, R. Kaesler, and S. LoDuca for their helpful comments in preparation of the second edition. I thank N. Arens, R. Gastaldo, J. Myers, G. Retallack, B. Tiffney, and S. Wing for their reviews of the new paleobotany chapter. I thank Lisa Leibold for all her editorial help with the second edition.

Donald R. Prothero
La Crescenta California
December, 2002

to the student: Why Study Fossils?

Fossil hunting is by far the most fascinating of all sports. It has some danger, enough to give it zest and probably about as much as in the average modern engineered big-game hunt, and danger is wholly to the hunter. It has uncertainty and excitement and all the thrills of gambling with none of its vicious features. The hunter never knows what his bag may be, perhaps nothing, perhaps a creature never before seen by human eyes. It requires knowledge, skill, and some degree of hardihood. And its results are so much more important, more worthwhile, and more enduring than those of any other sport! The fossil hunter does not kill, he resurrects. And the result of this sport is to add to the sum of human pleasure and to the treasure of human knowledge.

George Gaylord Simpson, *Attending Marvels,* 1934

At the beginning of any course, students often ask, "Why study this subject? What will I get out of this class?" Many subjects seem very abstract and intangible to students, and the relevance to their careers, or importance in their daily lives, is not readily apparent. Like many other topics in the curriculum, paleontology has had to fight to justify its existence. However, the benefits of paleontology are easy to enumerate:

1. **Biostratigraphy**—*Fossils are the only practical means of telling time in geology.* Radioisotopic decay methods, such as potassium-argon or uranium/lead dating, work only in rocks that have cooled down from a very hot state, such as igneous or metamorphic rocks. Most of geological history is contained in sedimentary rocks, which cannot be dated by radioisotopes. Consequently, fossils are the only practical method of determining the age of rocks in most geological settings. For a long time, the largest employers of paleontologists were oil companies, who relied heavily on biostratigraphers to tell them where to find oil. Modern civilization would have been impossible without them. No matter what fads come and go in geology, there will always be demand for paleontologists who can answer the basic question, "How old is it?"
2. **Evolution**—*Fossils are the only direct record of the history of life.* Although evolutionary biology has made enormous strides studying living organisms such as bacteria, fruit flies, and lab rats, these studies see evolution only in the thin slice of time known as the Recent. Fossils provide the only direct evidence of 3.5 billion years of the history of life, and in many cases, they suggest processes that might not be explainable by what is known from living organisms. Fossils provide a fourth dimension (time) to the biology of many living organisms. Many groups of organisms, such as conodonts and graptolites, are extinct and are known only from the fossil record.
3. **Paleoecology**—*Fossils can provide direct evidence of ancient environments.* Although many sedimentary rocks deposited in different environments look very similar, the fossils and trace fossils found within them are often their most diagnostic feature. They can be used to pinpoint the depositional environment more precisely than any other property of the sedimentary rock.
4. **Paleogeography**—*Fossils can be critical to determining ancient continental positions and connections.* Some of the earliest evidence for continental drift came from the similarities of fossils on different continents, and paleontological evidence is critical to any understanding of biogeography.
5. **Simple fascination**—*Fossils are interesting, in and of themselves.* Although the reasons listed above are important, most people become paleontologists because they love fossils and are fascinated by extinct organisms. In what other discipline but paleontology could a discovery only slightly larger than any previously known (a new gigantic dinosaur specimen) make the front page of the *New York Times?* Why is it that anything with dinosaurs in it (including one of the highest-grossing movies of all time, *Jurassic Park*) is immensely popular? Although dinosaurs are only a small part of paleontology, the popular fascination with things prehistoric can be extended even to the invertebrates of the Cambrian (witness the enormous popularity of trilobites, or the response to Stephen J. Gould's book *Wonderful Life*).

In short, there are many reasons, both practical and fun, for studying fossils. The eminent early twentieth-century paleontologist William Diller Matthew (writing in 1925 during the height of anti-evolutionism coming from the Scopes "Monkey" Trial) said it eloquently (and with the traditionally masculine language of his time, when there were few female paleontologists):

A few men, a mere handful scattered among the millions of civilization, devote their lives to collecting and studying fossils. A larger number take a more casual interest in the results of these studies. The vast majority have never heard of fossils or ask indifferently, "Why should anyone waste his time upon such useless studies?" This is the answer:

In the first place, what are fossils? They are teeth or bones or shell of animals found buried in solid rock. These fossils, remains of animals that have lived in past ages but no longer survive, are the records of the history of life. We collect and study and compare them so that we can reconstruct these extinct animals, so that we can find out, as far as may be, just how they differed from those that preceded and from those that succeeded them, how they lived and to what environment they were adapted. Our aim is to reconstruct the history of life during the vast periods of time that have elapsed since the first rocks were formed.

Current history is but a passing phase, a stage in the march of events, past, present, and future. We cannot follow present events without becoming keenly interested in the past, which explains the present, and in the future, which we can predict more certainly if we have an adequate knowledge of the past and the present. The more we know of these, the more clearly can we discern the laws that govern the orderly progress of events, the more definitely and positively can we perceive what is to come, at least in its broader outlines. Herein lies the great fascination of historical studies: in the attempt to synthesize and arrange the infinite multiplicity of events great and small, to find the underlying causes to whose interaction they may be ascribed, to test and prove the soundness of our theories by bringing them to bear upon other groups of events, above all to apply the acid test of fulfilment to our prophecies, the confirmation of our theories by new discoveries and forthcoming events. To read the future is the dearest wish of man and it can be done insofar as his knowledge and understanding of the past show whence we have come and whither we are going.

But history in the ordinary sense of the word deals with but a limited portion of the past of man. The world in which we live has a far wider scope and its history extends backward through enormous periods of time in comparison with the few thousand years covered by recorded human history. From these fossil records, the "documents" of earth history, it has been possible to build up a great and splendid science, secure and fixed in its massive foundations and its broader lines of structure, more doubtful and speculative in some of its lighter tracery and ornamentation. Those who, through field work and study, have been able to add brick by brick to extend and amplify its solid basis, who have learned the laws of its architecture and aided in building up its superstructure, who have at times been privileged to add some bright pinnacle or favorite cornice to its glittering towers—these men have come to love their science beyond all else. It is their home which they have helped to build, and its beauty and symmetry, its noble and appropriate proportions, and its perfection fill them with an ever-growing admiration and affection.

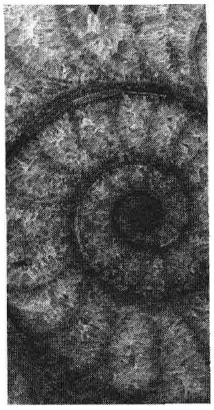
Do you wonder that the paleontologist, absorbed in contemplation of his splendid edifice, walks a little apart from the ways of men; that the little personal affairs and interests of the fleeting present which make up the world of his fellows, seem to him but gewgaws and trifles of no importance? His field of vision embraces the whole of life. His time scale is so gigantic that it dwarfs to insignificance the centuries of human endeavor. And the laws and principles which he studies are those which control the whole great stream of life, upon which the happenings of our daily existence appear but as little surface ripples.

Pre-eminent among the laws which govern the architecture of our world of life is evolution. To the zoologist the law of evolution appears as a theory, an explanation of the world of nature that lies about him. It is the only theory that really explains it, and it fits all the marvelously complex details of adaptation, the perfections and likewise the imperfections of structure of every animal and plant so perfectly and accurately that few or no zoologists can question the theory, however they may dispute about the precise method of its action. To the paleontologist, however, evolution appears not as a theory but as a fact of the record. He does not and cannot doubt the gradual development of diversely specialized races from a common ancestral stock through a long series of intermediate gradations, for he has before him all these stages in the evolution of the race preserved as fossils, each in its appropriate place in the successive strata of a geologic period. It is not a matter of deduction but of observation, at least in those races of animals whose fossil record has been discovered; for the rest it is a matter of obvious inference. Concerning the causes and methods of this evolutionary process he finds wide room for discussion; but of the fact, of the actuality of it he can have no doubt. Evolution is no more a theory to the man who has collected and studied fossils than the city of New York is a theory to the man who lives in it.

But, in truth, evolution is only one aspect of the order of nature, of the relations of cause and effect, of continuity of space and time, which pervade the universe and enable us to comprehend its simplicity of plan, its complexity of detail. The paleontologist, engaged in adding year by year to the mass of documents which record the history of life, in deciphering their meaning and interpreting their significance, has no more occasion to doubt its continuity and orderly development than the historian has to doubt the continuity and consecutive evolution of human history, or the student of current affairs to doubt that the events of today will result in the conditions of tomorrow.

Such is the value of palæontology. It provides an essential part of the evidence for scientific study of the rocks, which has made possible the huge expansion of the mining industries upon which our modern material civilization is so largely based. Its higher value lies in adding to our knowledge and aiding in our comprehension of the world we live in, in tracing the past history of life and finding in it the explanation of the present, in observing the ordered progress of evolution under natural law from the beginnings of the world down to the present day, in helping us to discern through a better knowledge of the past what may be the course of future events.

W. D. Matthew, 1925, *Natural History* 25(2):166–168.



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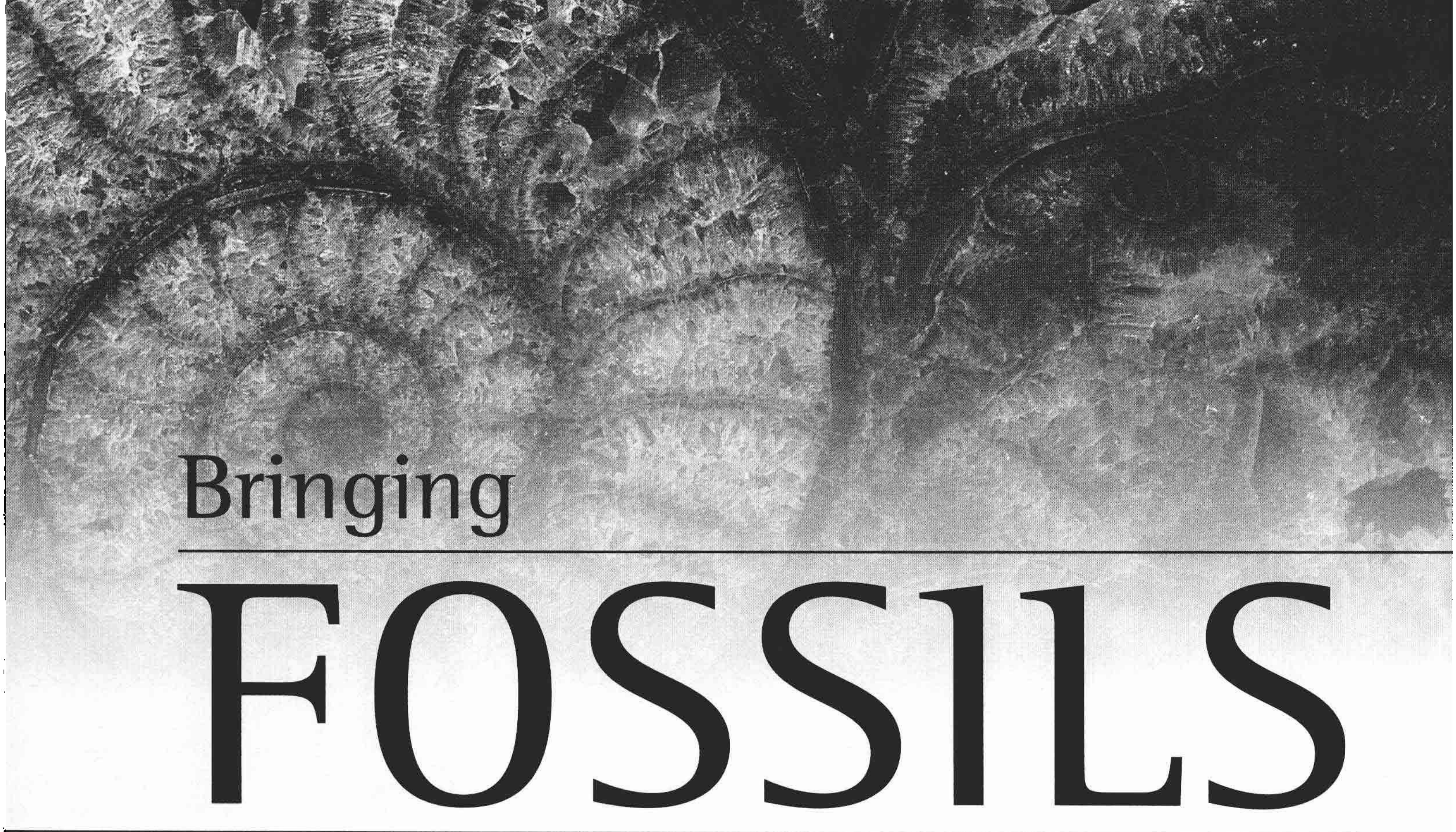
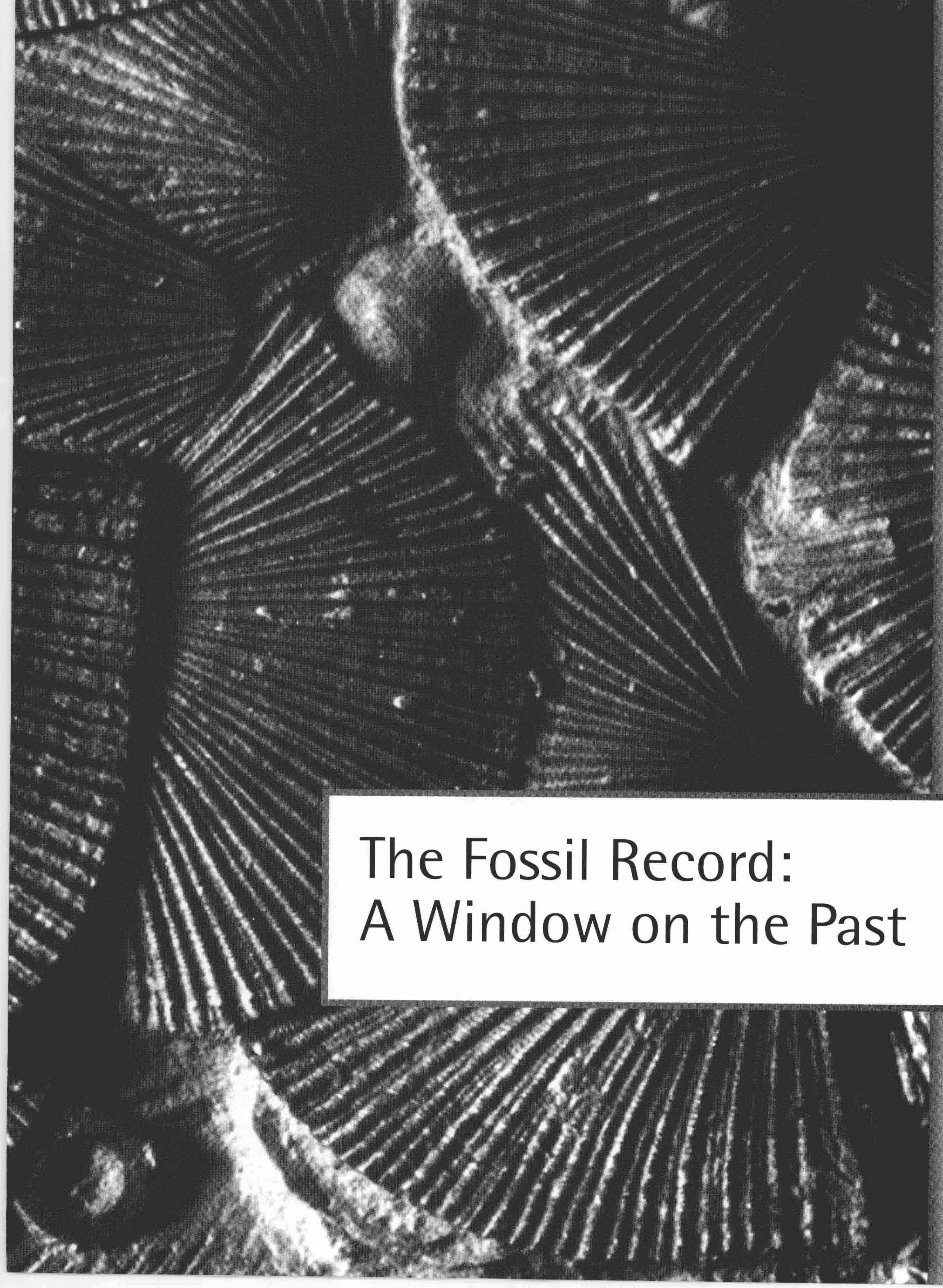


Bringing FOSSILS to Life

part one



The Fossil Record: A Window on the Past

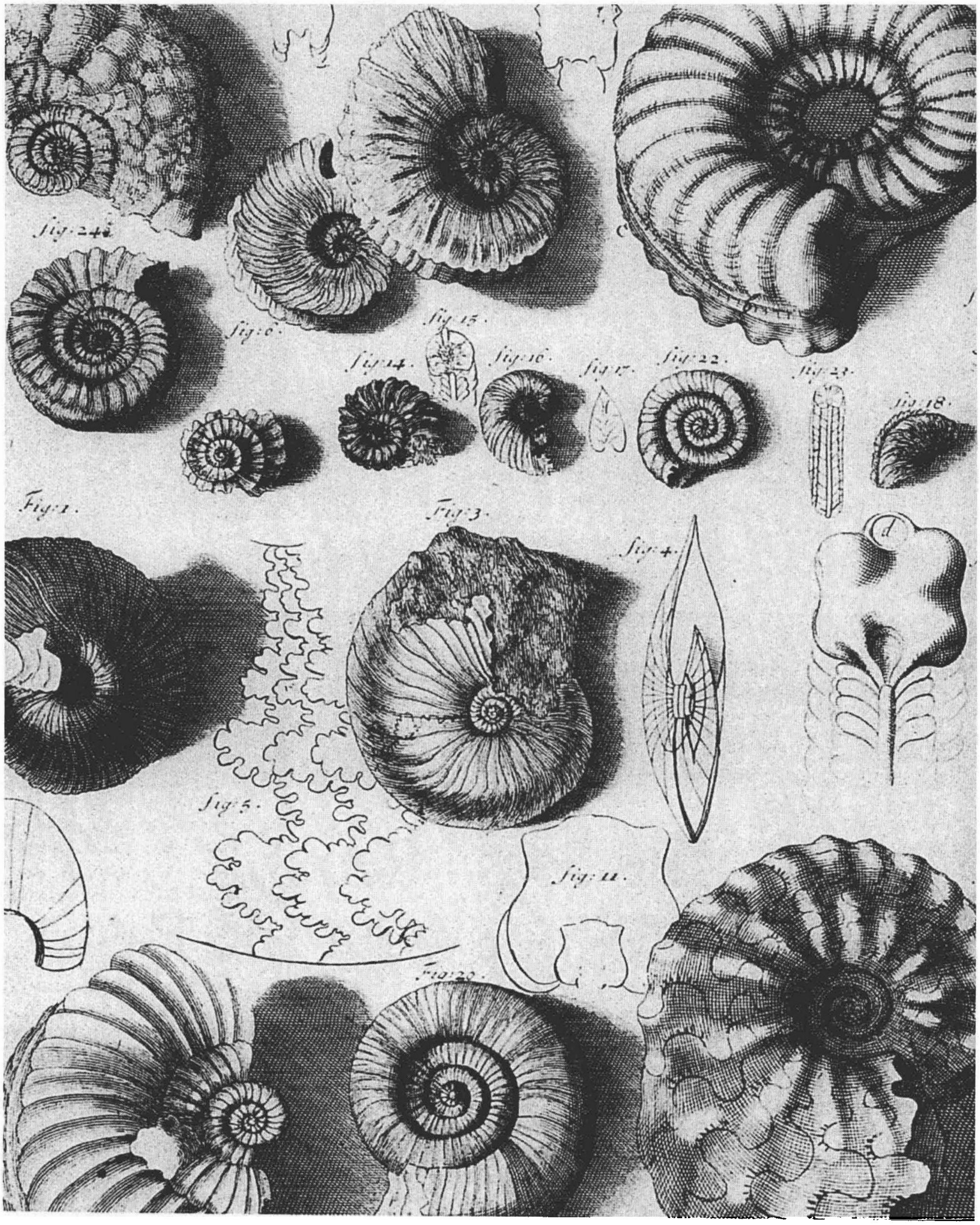


figure 1.1 Seventeenth-century illustrations of fossil ammonoids (*Cornua ammonis*, or "snake stones") drawn by the versatile scientist Robert Hooke, the father of microscopy and paleontology in Britain. (From the posthumous works of Robert Hooke, 1703.)

chapter 1

The Fossil Record

In the mountains of Parma and Piacenza multitudes of rotten shells and corals are to be seen, still attached to the rocks. . . And if you were to say that such shells were created, and continued to be created in similar places by the nature of the site and of the heavens, which had some influence there—such an opinion is impossible for the brain capable of thinking, because the years of their growth can be counted on the shells, and both smaller and larger shells may be seen, which could not have grown without food, and could not have fed without motion, but there they could not move.

And if you wish to say that it was the Deluge which carried these shells hundreds of miles from the sea, that cannot have happened, since the Deluge was caused by rain, and rain naturally urges rivers on towards the sea, together with everything carried by them, and does not bear dead objects from sea shores towards the mountains. And if you would say that the waters of the Deluge afterwards rose above the mountains, the movement of the sea against the course of the rivers must have been so slow that it could not have floated up anything heavier than itself.

Leonardo da Vinci, c. 1500

WHAT IS A FOSSIL?

When we pick up fossils in a roadcut, or see a dinosaur skeleton in a museum, we have no problem connecting it to some sort of extinct organism. We have been conditioned since our early education to interpret fossils as remains of extinct organisms, and it is hard for us to imagine any other explanation.

Centuries ago, however, such an interpretation was not automatic or even easy to make. The ancient Greeks interpreted the giant bones of mammoths as the remains of mythical giants, but were puzzled with seashells found hundreds of feet above sea level and miles inland. Had the sea once covered the land, or had these objects grown within the rocks like crystals do? In the sixth century B.C., Xenophanes of Colophon saw the seashells high in a cliff on the island of Malta and suggested that the land had once been covered by the sea. The oldest recorded statement that fossils are the remains of once-living animals that have been entombed in rocks was made by Xanthos of Sardis around 500 B.C. Aristotle (born 384 B.C.) suggested that the fossils of fish were remains of sea animals that had swum into cracks in rocks and were stranded there, and his ideas were influential for the next 2000 years.

From the late days of the Roman Empire, almost all people in Western society were raised to believe in the literal interpretation of the book of Genesis, and the stories of the six days of Creation and Noah's Flood colored their view of rocks and fossils. For those of us in the early twenty-first century, a fossil snail shell looks so similar to its living descendants that we cannot imagine any other explanation. We forget that most people of that time (other than fishermen) had limited familiarity with life on the bottom of the ocean. In fact, many fossils bear no resemblance to anything that fifteenth-century Europeans could have seen. Until the living chambered nautilus was discovered in 1829, who could imagine that the coiled objects known as *Cornua ammonis* ("Horns of Ammon") "serpent stones" were relatives of the squid and octopus with a coiled, chambered shell (Fig. 1.1)? Who could imagine that the strange bullet-shaped objects known as a belemnites were also related to squid? Even today, most people who pick up the odd cylindrical objects known as crinoid columnals (Fig. 1.2) do not recognize them as relatives of the sea star or sea urchin, because only a few people have seen the rare stalked crinoids that still live on the seafloor. For centuries, scholars were impressed with the star-shaped patterns in the centers of the columnals (and the radial patterns in fossil corals), and thought they had been produced by thunderbolts or fallen from the sky; they were known as "star stones" (*Lapis stellaris* or *Astroites stellis*).

During the Middle Ages and Renaissance, learned men began to speculate on the meaning of fossils, producing a wide range of interpretations. Originally, the word "fossil" (from the Latin *fossilis*, "dug up") applied to any strange object found within a rock. These included not only the organic remains that we call fossils, but also crystals and concretions and many other structures that were not organic in origin. Most scholars thought that fossils had formed spontaneously within the rock; those that resembled living organisms were thought to have crept or fallen into cracks and then converted to stone. Others thought they were grown in rocks from seeds, or were grown from fish spawn washed

figure 1.2 Conrad Gesner's 1565 illustrations of bullet-shaped belemnites and crinoid columnals, neither of which looked like marine organisms familiar to Renaissance Europeans. To many of them, including Gesner, the star-like pattern of some crinoid stems suggested that they might have been produced by falling stars.

into cracks during Noah's Flood. Many scholars thought they were supernatural, "pranks of nature" (*lusus naturae*), or "figured stones" produced by mysterious "plastic forces." Still others considered them to be works of the Devil, placed in the rocks to shake our faith. As quaint and comical as these ideas seem to us today, in their own time they were perfectly rational for people who believed in a literal interpretation of Genesis, and thought the Earth had been created just as we see it about 6000 years ago, with little or no change since then except for decay and degradation due to Adam's sin.

Some Renaissance men, however, were ahead of their time. Around 1500, Leonardo da Vinci (1452–1519) recognized that the fossil shells in the Apennine Mountains of northern Italy represented ancient marine life, even though they were miles from the seashore. Unlike his contemporaries who thought they had been washed there by the Flood, da Vinci realized that they could not have washed that far in 40 days, and many shells were too fragile to have traveled that far. Many shells were intact and in living position and resembled modern communities found near the seashore; clearly they were not transported. In some places, there were many shell beds separated by unfossiliferous strata, so they clearly were not due to a single Flood. However, most of da Vinci's ideas remained in his unpublished notebooks, and even if he had tried to publicize them, they would not have been accepted at that early date.

In 1565, the Swiss physician Conrad Gesner (1516–1565) published *De rerum fossilium* ("On the nature of fossils"), the first work that actually illustrated fossils. With this step, the vague verbal descriptions of earlier authors could be made more precise (Fig. 1.2). Gesner based his descriptions on both his own collections and those of his friends, beginning the modern tradition of scientific exchange, analysis, and comparison. Gesner was correct in comparing most fossils to their living relatives, but he thought that some objects (crinoid columnals, belemnites) were formed by mineral precipitation. Like most of his contemporaries, Gesner interpreted fossils as supernatural representations of Neoplatonic "ideal forms" and did not explore most of the implications that would seem obvious to us today.

Through all of these early writings, four main questions about fossils were disputed:

1. Are fossils really organic remains?
2. How did they get into the rocks?
3. When did they get there—as the rock was being formed, or long after?
4. How did they become petrified?

Essentially modern answers to all these questions were first proposed by a Dane named Niels Stensen, known to later generations by the Latinized version of his name, Nicholaus Steno (1638–1686). Steno was the court physician to the Grand Duke of Tuscany, so he had ample opportunity to see the shells in the rocks of the Apennine Mountains above Florence. In 1666, he had a chance to dissect a large shark caught near the port town of Livorno. A close look at the mouth of the shark showed that its teeth closely resembled fossils known as "tongue stones" (***glossopetrae***), which had been considered the petrified tongues of snakes or dragons (Fig. 1.3). Steno realized that tongue stones were actually ancient shark teeth, and that fossil shells were produced by once-living organisms.

In 1669, Steno published *De solido intra solidum naturaliter contento dissertationis prodromus* ("Forerunner to a dissertation on a solid naturally contained within a solid"). The title may seem peculiar at first until you realize the central problem that Steno faced: how did these solid objects get inside solid rock? Steno realized that the enclosing sandstone must have once been loose sand and was later petrified into sandstone. With this idea, he overturned the longstanding assumption that all rocks had been formed exactly as we see them during the first days of Creation. Steno extended this insight into a general understanding of relative age of geological features. Fossils that were enclosed in rock that had been molded around them must be older than the rock in which they lie. On the other hand, crystals that clearly cut across the preexisting fabric of a rock must have grown within the rock after it formed. From this, Steno generalized the principles of superposition, original horizontality, and original continuity that are the fundamental principles of historical geology and stratigraphy.

As the *Prodromus* was being published, Steno converted to Catholicism and gave up his scientific interests, so the "forerunner" was never followed by the promised dissertation. He was eventually made the Bishop of Titiopolis, a region in eastern Europe that had not converted to Catholicism, so he never lived there or ministered to its people.

figure 1.3 Steno's 1669 illustration of the head of a shark, showing that the "tongue stones" or *glossopetrae* are extremely similar to modern shark teeth.

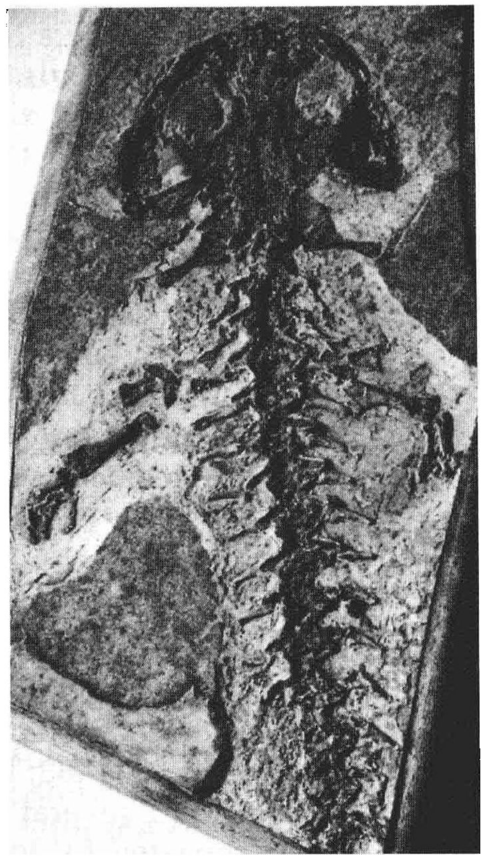


figure 1.4 Johann Scheuchzer's *Homo diluvii testis*, or "Man, a witness of the Flood," described in 1726. Unfortunately, Scheuchzer's anatomical skills were not up to his Biblical knowledge, since it is actually the fossil of a giant salamander.

Instead, he returned to Denmark to serve the Church for the rest of his life.

About the time that Steno's writings appeared, a pioneering British scientist came to similar conclusions. Robert Hooke (1635–1703) is better known as the "Father of Microscopy," because he built one of the first microscopes and made the first drawings of microorganisms and the details of cellular structure. In 1665, Hooke made observations of many natural objects, including the first accurate drawings of fossils, which were published posthumously in 1705 (Fig. 1.1). Hooke even suggested that fossils might be useful for making chronological comparisons of rocks of similar age, much as Roman coins were used to date ancient historical events in Europe. He speculated that species had a fixed "life span," for many of the fossils he studied had no living counterparts. This was one of the first hints of the extinction of species, because few people at that time doubted that all the species on earth had been created 6000 years ago and were still alive.

However, most of Hooke's and Steno's ideas would not be accepted for another century. In the early 1700s, ideas about fossils were still heavily influenced by the Bible. For example, in 1726 the Swiss naturalist Johann Scheuchzer (1672–1733) described a large fossil as "the bony skeleton of one of those infamous men whose sins brought upon the world the dire misfortune of the Deluge." He named it *Homo diluvii testis* ("Man, a witness of the Flood"). Unfortunately, since comparative anatomy was not very sophisticated at this time, his specimen turned out to be a giant fossil salamander (Fig. 1.4). Another scholar, Dr. Johann Beringer (1667–1740), dean of the medical school of Würzburg, Germany, was fascinated with the "petrifactions" that collectors had brought him from the local hills. Some bore resemblance to frogs, shells, and many other natural objects; others had stars and many other curious shapes and patterns. In 1726, as Beringer was about to publish a massive monograph of his "figured stones," two colleagues whom Beringer had offended confessed to the prank. They had carved the figured stones, correctly guessing that he was gullible enough to accept them, but their warning came too late to stop publication of the hoax. Beringer died a ruined man, spending his last pfennig trying to buy back all the copies of his book.

By the mid 1700s, however, naturalistic concepts of fossils began to prevail. When Linnaeus published the first edition of his landmark classification of all life, *Systema Naturae,* in 1735, fossils were treated and named as if they were living animals. Around 1800, Baron Georges Cuvier (1769–1832) made great strides in comparative anatomy, skillfully showing that certain anatomical features, such as claws and sharp teeth, or hooves and grinding teeth, were correlated. He became so adept at this knowledge that he started the paleontological tradition of predicting unknown parts of the animal by comparison to the known anatomy of close relatives. Cuvier also showed that the bones of mastodonts and mammoths were the remains of elephant-like beasts that clearly had to be extinct, because the explorers had not found them on even the most remote continents. Prior to that time, most people could not accept the fact of extinction, because it went against their notion of Divine Providence. After all, if God watched after the little sparrow, surely He would not allow any of his creations to go extinct? Cuvier went on to become the founder of comparative anatomy and vertebrate paleontology, and brought much of paleontology out of Biblical supernaturalism and into a firm comparative basis.

Just before 1800, British engineer William Smith (1769–1839) was surveying England for the great canal excavations prompted by the Industrial Revolution. From these fresh canal exposures and regular visits to mines, Smith began to realize that fossils showed a regular pattern—each formation had a different assemblage of fossils. As he wrote in 1796, he was struck by "the wonderful order and regularity with which nature has disposed of these singular productions [fossils] and assigned each to its own class and peculiar Stratum." Smith was so good at recognizing the fossils of each formation that he amazed private collectors by correctly identifying the layers from which their specimens had come. He used this understanding of faunal succession to map the strata of England and Wales, culminating in the first modern geological map, which was finally published in 1815. At about the same time, Cuvier and his colleague Alexandre Brongniart were mapping fossils and strata in the Paris Basin and also began to realize that there was a regular succession of fossils that differed from formation to formation. In two different regions (apparently independently) each made the discovery that eventually led to our modern concepts of biostratigraphy as a tool for unraveling earth history.

By the time of the publication of Darwin's *On the Origin of Species* in 1859, the realization of the complexity of the fossil record had reached the point where few scholars took Noah's Flood literally. However, the notions about what the fossil record tells us about the history and evolution of life has continued to change, as we shall see in later chapters.

HOW DOES AN ORGANISM BECOME A FOSSIL?

Being a paleontologist is like being a coroner except that all the witnesses are dead and all the evidence has been left out in the rain for 65 million years.

Mike Brett-Surman, 1994

There are over 1.5 million named and described species of plants and animals on Earth at this moment, and probably many more that have never been named or described; some estimates place the total number at about 4.5 million species. Yet the fossil record preserves only a small fraction of this total and does so in a very selective manner. Some groups of organisms with hard parts (such as shells, skeletons, wood) tend to fossilize readily and much is known about their past. Many others are soft-bodied and rarely if ever fossilize, so paleontology has little to say about their history. The study of how living organisms become fossilized is known as **taphonomy** (Greek for "laws of burial").

There are several ways to get a sense of just how unlikely fossilization can be. For example, modern biological studies show that the typical sea bottom is often dense with shells. One-quarter of a square meter of seafloor off Japan (Thorson, 1957) yielded 25 individuals of a large bivalve (*Macoma incongrua*), 160 of a smaller cockle shell (*Cardium hungerfordi*), and 12 of the tusk shell (*Dentalium octangulatum*). The average age of these molluscs is 2 years. At this rate, there would be 1000 shells in just 10 years, or one hundred million in a million years—over one-quarter of a square meter! Extrapolated over the whole seafloor and over geological time, this suggests that a staggering number of shells could have been fossilized. In fact, that tiny area of seafloor near Japan could produce more fossilizable shells than is actually known from the entire fossil record! Clearly, most organisms do *not* become fossils.

The study of taphonomy has become very popular in the last 20 years for one simple reason: to understand and interpret the preserved fossil record, you must first determine how taphonomic processes have biased your sample. From the moment an organism dies, there is a tremendous loss of information as it decays and is trampled, tumbled, and broken before it is buried. The more of that lost information that we can reconstruct, the more reliable our scientific hypotheses are likely to be. In this sense, every paleontologist has to act as a coroner/forensic pathologist/detective, determining what killed the victim and trying to reconstruct the events at the "scene of the crime."

The first step is to determine just what type of fossilization has taken place. Most fossils have been dramatically altered from the original composition of the specimen, and often their original shape and texture are hard to determine unless one has some idea of what took place. The major types of preservation processes are discussed next.

Unaltered Remains

In a few exceptional cases, organisms are preserved with most of their original tissues intact. Ice Age woolly mammoths have been found thawing out of the Siberian tundra with all their soft tissues essentially freeze-dried, including their last meals in their digestive tracts (Fig. 1.5A).