

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

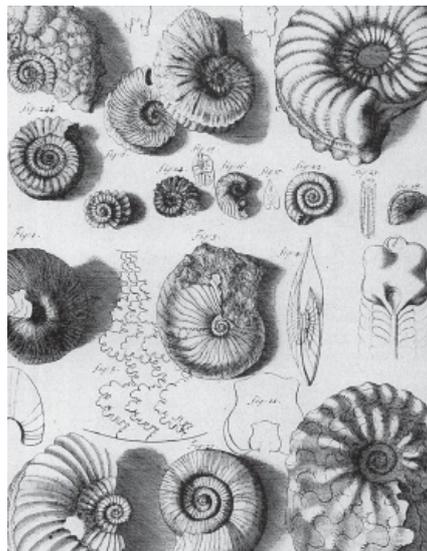


FIGURE 1.1 Seventeenth-century illustration of fossil ammonoids (*Cornua ammonis*, or “snake stones”) drawn for the posthumously published monograph of Robert Hooke (1703). Hooke was one of the most versatile scientists of his time and the father of both paleontology and microscopy in Britain.

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 by 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 as 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 the sea had once covered the land. The oldest recorded statement that fossils are the remains of once-living animals that were entombed in rocks was made by Xanthos of Sardis around 500 B.C. Aristotle (b. 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 European society were raised to believe in the literal interpretation of the book of Genesis, and the stories of the 6 days of Creation and Noah’s Flood colored their view of rocks and fossils. For those of us at the beginning of the 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 the coiled objects known as *Cornua ammonis* (Horns of Ammon) or “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 belemnites (fig. 1.2) 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 had fallen from the sky; they were known as “star stones” (*Lapis stellaris* or *Astroites stellis*).



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 be produced by falling stars.

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 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 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 the fossils 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. 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 with 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, Nicolaus Steno (1638–1686). Steno was the court doctor to the Grand Duke of Tuscany, so he was one of the most scientifically educated people of his time. He also 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.

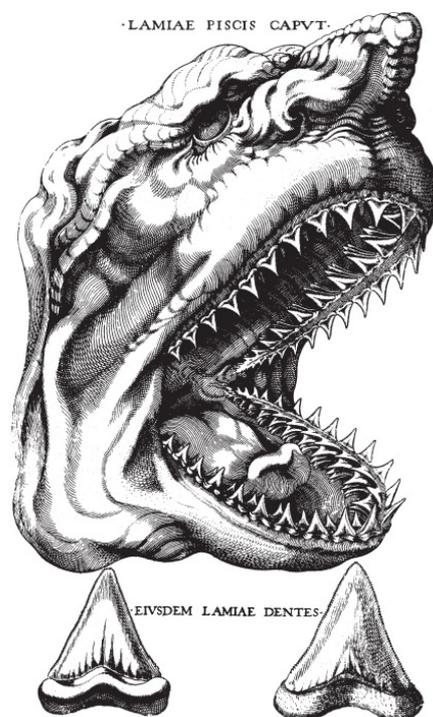


FIGURE 1.3 Steno's 1669 illustration of the head of a shark, showing that the “tongue stones” or *glossopetrae* are extremely similar to modern shark teeth.

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 solid objects (such as fossils or crystals) 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 geologic features. Fossils 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 pre-existing 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 Titipolis, a region in eastern Europe that had not converted to Catholicism, so he never lived there or ministered to its people. 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 previously 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, because comparative anatomy was not very sophisticated at this time, his specimen turned out to be a giant fossil salamander (fig. 1.4). Another scholar, Johann Beringer (1667–1740), dean of the medical school of Wurzburg, Germany, was fascinated with the “petrifications” 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.



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.

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 with the known anatomy of close relatives. Cuvier also showed that the bones of mastodons 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 (see [chapter 6](#)). 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.

In the 1790s, 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, which culminated in the first modern geologic map, 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) both Smith in England and Cuvier and Brongniart in France made the discovery that eventually led to our modern concepts of biostratigraphy as a tool for unraveling Earth's 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 to as many as 10 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: “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 100 million in a million years—over one-quarter of a square meter! Extrapolated over the whole seafloor and over geologic 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 40 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 we can reconstruct, the more reliable our scientific hypotheses are likely to be. In this sense, every paleontologist has to act as a crime scene investigator/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). Some were so fresh that humans and animals could eat their 30,000-year-old meat with no ill effects. An Ice Age woolly rhinoceros was found intact in a Polish oil seep; the petroleum pickled the specimen and prevented decay. These examples are extremely rare, but when they occur, they give us detailed insight into the color, diet, muscles, hair texture, and other anatomical features that paleontologists seldom see.

Some fossils have decayed so that the soft tissues are gone, but their hard parts are unaltered. The famous tar pits of Rancho La Brea in Los Angeles are full of 35,000- to 9000-year-old bones that retain their original composition, but are pickled in tar, so they are black and smell like petroleum (fig. 1.5B). However, enough of their original chemistry remains that scientists have been able to extract their DNA and compare it with that of living relatives. Similarly, many shells (particularly those of Pleistocene age) still have their original shell material unaltered, including the iridescent “mother of pearl” aragonitic layer that frequently lines their interior. In some cases, Cretaceous ammonites have been found with their original aragonite (*nacre*, or “mother of pearl,” the less stable form of calcium carbonate) intact, but there are few fossils much older than this that retain their original aragonite.

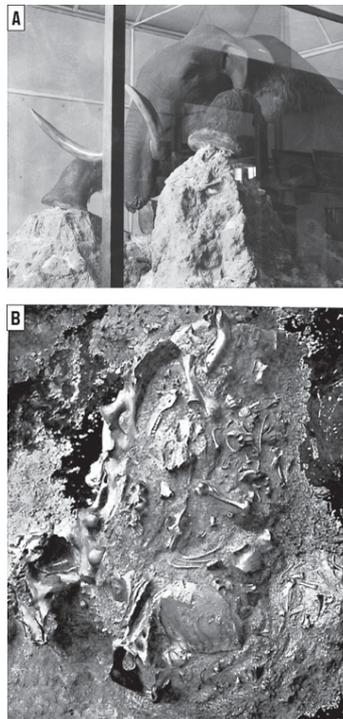


FIGURE 1.5 (A) A frozen mammoth discovered in 1901 in Beresovka, Siberia, was essentially unaltered, except for freezing. It still had its last meal in its mouth and a full stomach. Most of the skin and flesh of the head and trunk had been eaten by wolves, even though it was 30,000 years old. (Image #296538, courtesy of the American Museum of Natural History Library.) (B) Typical 40,000-year-old fossil bones from the Rancho La Brea tar pits in Los Angeles, California. They still retain their original bone material, but have been pickled in tar. (Courtesy of the Natural History Museum of Los Angeles County.)

Preservation in amber is a special case (fig. 1.6A). These specimens are fossilized when tree resin oozes downward and entraps insects, spiders, and even frogs and lizards. The resin then hardens and forms a tight seal around the organism. Most specimens are only carbonized films of insects and spiders, but some are so well preserved that their original biochemicals are still intact. Some of these molecules of the insect's body have been successfully extracted and sequenced, almost as depicted in the movie *Jurassic Park*, but most of the genetic material is so incomplete that we will never be able to reconstruct a complete organism. Unlike *Jurassic Park*, however, it is not possible to sequence the DNA in the blood in the stomach of mosquitoes; that is pure science fiction.

Permineralization

Many biological tissues are full of pores and canals. The bones of animals are highly porous, especially in their marrow cavity, and most wood is full of canals and pores. After the soft parts decay, these hard parts are buried and then permeated with groundwater that flows through them. In the groundwater, there could be dissolved calcium carbonate or silica, which precipitate out and fill up the pores, completely cementing the bone or wood into a solid rock. Unlike replacement (discussed below), new material comes in, but none of the original material is removed. The famous multicolored fossil logs of the Petrified Forest in Arizona (fig. 1.6B) are permineralized by silica, and many other examples of petrified wood and bone are permineralized by carbonate. Permineralization can be so complete that even the details of the cell structure are preserved.

Recrystallization

Some shells are made of relatively unstable minerals, such as aragonite. Once the shells leave surface conditions, most aragonite reverts to the more stable form of calcium carbonate, the mineral calcite (fig. 1.7). In other cases, shells made out of tiny crystals of calcite recrystallize into larger crystals. In these cases, the original shape of the fossil is preserved, but the difference in the texture is apparent under a microscope.

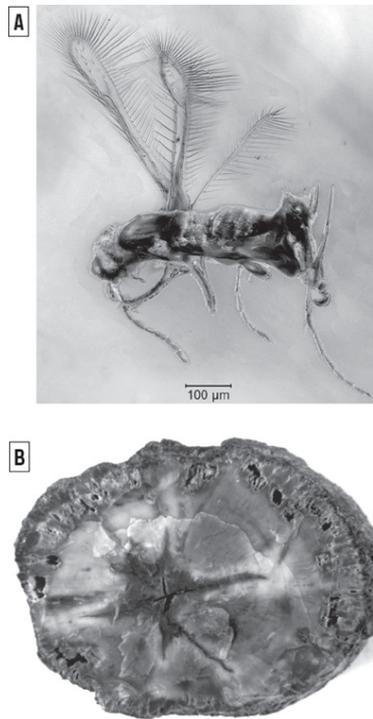


FIGURE 1.6 (A) This fly trapped in amber preserves even the finest details of wings and bristles, but most of the original organic material has degraded. (From Wikimedia Commons.) (B) Petrified wood from the Triassic Petrified Forest of Arizona has been completely permineralized with silica, preserving the delicate plant tissues and cell structure. (Photo by the author.)

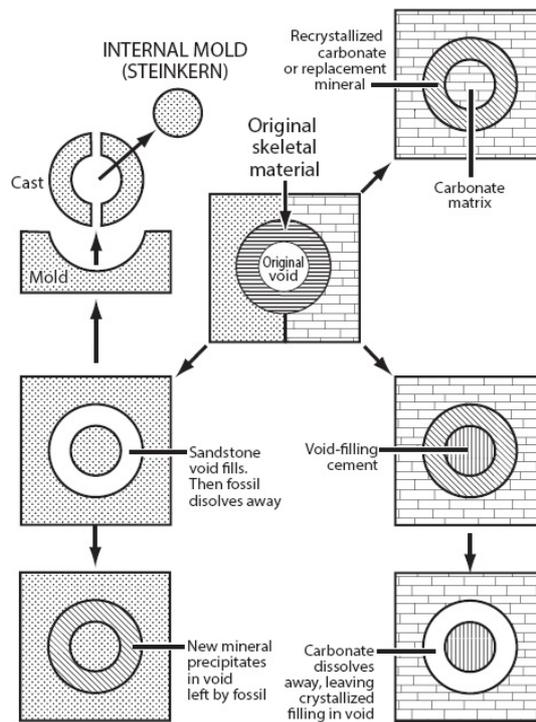


FIGURE 1.7 Many different diagenetic processes can change the original material into a fossil. If it is preserved in sandstone (stippled pattern), the sand may fill the original cavity in the fossil, leaving a cast. If the original skeletal material dissolves away, a void may be left that can be filled by another mineral. If it is preserved in limestone (brick pattern), fine-grained carbonate mud may fill the original void, or it may be filled by precipitation of cement (which can be calcite, but also silica or other minerals). If the original skeletal material was carbonate, it usually recrystallizes to coarsely crystalline calcite, but it may also dissolve away, leaving a void.

Dissolution and Replacement

As water seeps through sediments filled with shells or bone, there is also a tendency for the original material to dissolve (fig. 1.7). If the fossil dissolves and leaves a void, then the shape of the fossil is preserved in the surrounding sediments. The internal filling of this specimen is known as an internal mold (fig. 1.8A) or **steinkern** (German: “stone cast”). The external mold of the specimen is often also preserved. In other cases, the void is

filled with sediment and a natural cast of the fossil is formed, mimicking the original in surprising detail. Original bone or shell material can also be replaced without leaving a void. In these cases, the original calcite, aragonite, or phosphate is dissolved away atom by atom, and another mineral precipitates almost immediately in its place. This is easiest to detect when a fossil is made of some mineral that is clearly not original, such as calcitic brachiopods now made of silica or pyrite (fig. 1.8B).

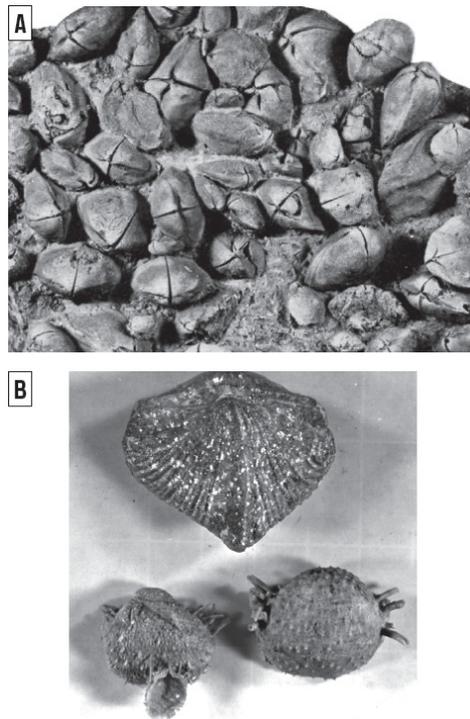


FIGURE 1.8 (A) Internal molds formed by filling the cavity left by a dissolved fossil are known as *steinkerns*. In this specimen, the shell of these pentamerid brachiopods has been dissolved away, leaving a steinkern with clefts where the internal partitions once were. (B) All articulate brachiopod shells are originally made of calcite, but these specimens have been replaced by pyrite (top) and silica (bottom). In the latter case, the siliceous replacement allows the specimen to be etched from limestone using acid and preserves the delicate spines. (Photos by the author.)

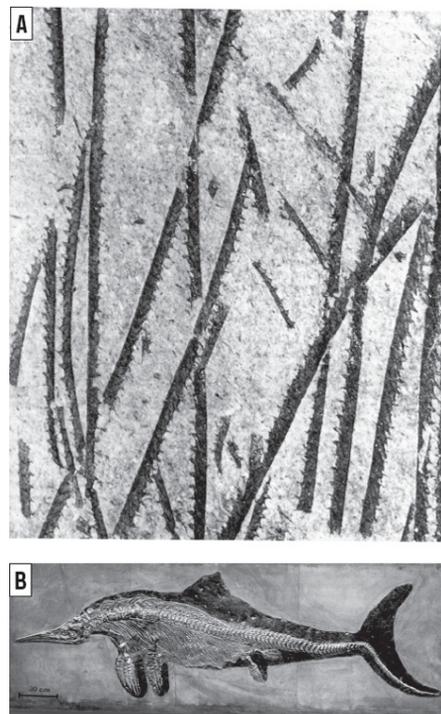


FIGURE 1.9 (A) Carbonized films are all that remain of most graptolite fossils, although they may still preserve enough detail to be identifiable. These graptolites have also been aligned by currents. (Photo courtesy of R. B. Rickards.) (B) The body outline of this ichthyosaur, a marine reptile, is preserved in a carbonized film around the skeleton. (Photo courtesy of R. Schoch, Staatliches Museum für Naturkunde, Stuttgart.)

Carbonization

Many fossils are preserved as thin films of carbon on the bedding planes of sandstones and shales (fig. 1.9). When the organism dies, most of the volatile organic materials and gases disperse and leave a residue of coal-like carbon, in the form of a black film that preserves the outline and sometimes the detailed structures of the organism. This kind of preservation is typical of most plant fossils; indeed, coal is the accumulated carbonized films of countless plants. There are many examples of carbonized animal fossils, especially among the graptolites (fig. 1.9A), that are virtually always preserved as carbonized films. There are also Eocene fossil insects preserved in extraordinary quality in places such as Florissant, Colorado, and the body outlines of ichthyosaurs from the Jurassic are found in Holzmaden Shale in Germany (fig. 1.9B).

WHAT FACTORS AFFECT THE FOSSILIZATION POTENTIAL OF AN ORGANISM?

Now let us turn to our richest geological museums and what a paltry display we behold! That our collections are imperfect is admitted by everyone. Many fossil species are known from single and often broken specimens. Only a small portion of the earth has been geologically explored, and no part with sufficient care. Shells and bones decay and disappear when left of the bottom of the sea where sediment is not accumulating. We err when we assume that sediment is being deposited over the whole bed of the sea sufficiently quickly to embed fossil remains.

—Charles Darwin, *On the Origin of Species*, 1859

As the list of modes of preservation suggest, there are many factors that affect the preservation potential of a dead organism. These factors operate at different stages in the “life history of a fossil.” Figure 1.10 shows a diagrammatic summary of the sequence of such processes. From the original complete assemblage of living organisms, known as a “life assemblage” or **biocenosis**, many events can occur that screen out certain organisms, leaving a much smaller death assemblage or **thanatocenosis**.

The process of breakup and decay of organisms immediately after death is known as **necrolysis** (literally, “breakup at death”). For example, the thanatocenosis on a modern seafloor will consist mostly of durable mollusc shells; all the soft-bodied invertebrates in the living biocenosis, such as sea jellies and worms, have decayed. Numerous studies have documented the biases inherent in the processes of death and decay and estimated the preservation potential of various marine invertebrates. For example, Johnson (1964), Stanton (1976), and Schopf (1978) censused the marine invertebrate fauna in three different regions (Tomales Bay, California; the southern California shelf; and Friday Harbor, Washington, respectively), and then estimated which organisms had the highest preservation potential. All three studies concluded that 25% to 30% of the fauna is likely to be preserved in the fossil record, with snails and clams having the best potential, and the soft-bodied groups such as flatworms, segmented polychaete worms (which may make up 40% of the species in modern shallow marine habitats), and other worm-like organisms (sipunculids, phoronids, and echiurids) having very little chance of fossilization. Some arthropods (such as heavy-shelled crabs and barnacles) may fossilize, but other thin-shelled crustaceans (such as shrimp) rarely do. A few thick-shelled echinoderms (such as sea urchins) fossilize, but sea stars and brittle stars have little chance of becoming fossils.

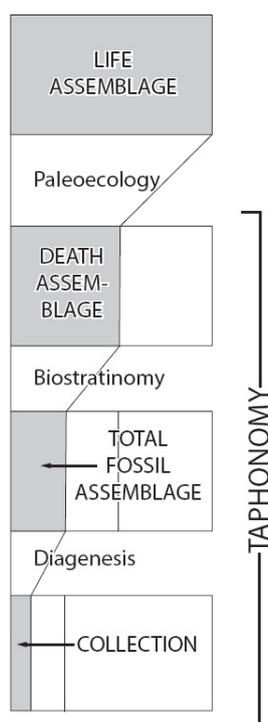


FIGURE 1.10 Diagrammatic summary of the processes of fossilization. At each step, a larger percentage of the original

assemblage is lost, until only a small fraction remains (gray area).

In addition, Schopf (1978) found that there were differences based on substrate and ecology as well. Organisms living on mud, sand, or rocky substrates appeared to fossilize almost equally well, although muddy bottoms have the best potential (because they represent quiet water with few energetic currents) and rocky habitats the worst (because they are seldom buried, and the wave pounding breaks up shells quickly). Even more striking was the difference between ecological types. About 67% of the sedentary organisms (herbivores and filter feeders) are fossilized, but carnivores and mobile detritus feeders are much less frequently preserved (16% to 27% of the taxa). Schopf pointed out that herbivores and filter feeders tend to have heavier skeletons, or may even be solid masses of calcite (such as corals), whereas detritus feeders and carnivores have much lighter and less durable skeletons, because they must move around to find their food. An estimate of the ratio of herbivores to carnivores from such data would be distorted and would not reflect true biological ratios of herbivores to carnivores.

Kidwell (2001) looked at 85 different data sets of marine molluscs, comparing living assemblages with the death assemblages represented by the shells. She found that, although the absolute numbers varied between samples, the most abundant organisms in the living sample were also those in the death assemblage, and the relative rank of most abundant species from most to least abundant was still preserved. In some cases, the relative abundance of organisms was higher in death assemblages, because the assemblages averaged a long interval of time (time-averaging) and tended to accumulate some of the rarer taxa. In fact, three species not found in the live assemblage were found in the death assemblage, so even rare taxa are sampled over long enough time intervals. This simple relationship is made even stronger when you change sieve size to allow the smallest shells to be included. In such cases, you get even better sampling, because juveniles are included, although in some cases live samples might be distorted relative to death assemblages if there has been a recent influx of larval shells.

After a death assemblage accumulates, many other factors operate on the hard parts to break them up and scatter them around, so an even smaller percentage ends up buried for future fossilization. These processes occur after necrolysis and are known as **biostratinomy** (loosely, “the laws by which living things become stratified”). These agents of destruction can be biological, mechanical, or chemical.

Biological Agents

Biological agents are the most important factor in most environments, both marine and terrestrial. Both predators and scavengers are very active in breaking up shells and bones to extract almost all the useful nutrition out of them. On the seafloor, a variety of organisms (especially fish, crabs, and lobsters) are effective in cracking shells to extract their food content. In an interesting set of experiments, Plotnick (1986) buried dead shrimp in marine sediment and then monitored their breakup. He found that scavengers (probably crabs) broke most of them up very quickly, even if they were buried as deep as 10 cm. Burrowing organisms were also very important in disturbing, breaking up, and consuming the carcasses. Only if they were buried deeper than 10 cm in relatively anoxic waters did the shrimp carcasses last, but eventually even these decayed due to bacterial action. A variety of similar studies in experimental taphonomy were summarized by Briggs (1995).

In addition to predators and scavengers breaking shells to extract soft parts for food, the shells themselves are subject to other biological agents of destruction. The most important of these are organisms that use the shell as a substrate or as a source of food or nutrients. A variety of organisms, including boring algae, boring sponges, worms, and bryozoans, erode holes and canals in dead shells and eventually weaken them so that they fall apart.

On land, a variety of predators and scavengers work very quickly to break up carcasses or vegetation. Once a tree falls in the forest, a wide variety of organisms, from termites, ants, beetles, and worms, to fungi and bacteria of various kinds reduce it to organic material that can be recycled back into the food chain. Studies of animals on the African savanna have shown that there is a distinct pecking order among predators and scavengers (fig. 1.11). After lions bring down their prey, they consume not only the best meat, but may even break some bones. Soon thereafter, the hyenas and jackals move in to scavenge the remaining meat and break up the bones for their marrow. The vultures hover nearby, getting whatever scraps then can. Finally, the ants and dermestid beetles strip the bones of the very last scraps of soft tissue, including tendons and cartilage. But these scavengers are not the only important biological agents of destruction. If the bones remain exposed, they are likely to be trampled by herds of antelope or zebra and quickly scattered around and reduced to splinters.

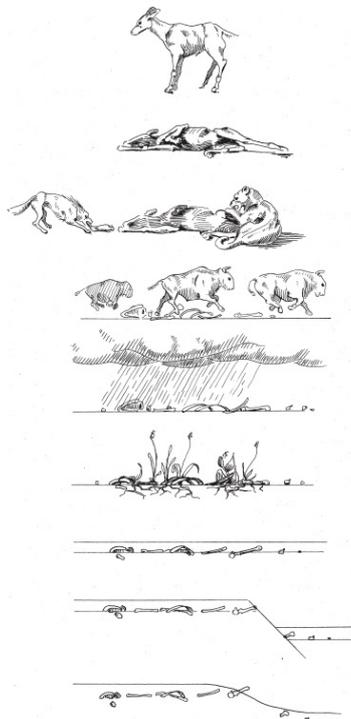


FIGURE 1.11 The processes of death, decay, scavenging, and burial act upon organisms in the African savanna, such as on this antelope. Only a tiny fraction of its bones ever have a chance of making it into the fossil record. (Reprinted by permission of the publisher from *Life History of a Fossil*, by Pat Shipman, Cambridge, Mass.: Harvard University Press. Courtesy of Pat Shipman.)

In summary, the key factor that prevents biological destruction is *rapid burial*.

Mechanical Agents

Mechanical agents of destruction, such as wind, waves, and currents, can be very important. These processes are most effective in shallow waters, where both waves and storms have their highest energies (Norris, 1986). In the marine environment, a number of studies (Driscoll, 1967, 1970; Driscoll and Weltin, 1973; Stanton, 1976; Warne et al., 1976) have simulated the processes of mechanical breakup of skeletons. One of the earliest, simplest, and most meaningful studies of these processes was performed by Chave (1964). He placed the skeletal parts of a number of marine invertebrates in a tumbling barrel with chert pebbles (the same tumbler that rockhounds use to polish and round precious stones) and then tumbled them for over 100 hours (fig. 1.12). As expected, thin-shelled organisms, such as coralline algae, bryozoans, echinoids, and jingle clams and razor clams, broke up in minutes or at most in a few hours. Thicker corals, bivalves such as mussels and oysters, and some snails were more durable, lasting up to 50 to 70 hours. The most durable were thick-shelled snails and clams, such as the round snail *Nerita* and the clam *Spisula*. Shell texture was also important. The densest, most fine-grained shells were the most durable, but skeletons with coarsely crystalline structure (such as oysters) or porous structure (such as corals) were less durable, even if they were relatively thick.

Kidwell and Baumiller (1990) further modified Chave's pioneering experiment to assess the effect of decay, temperature, and oxygen content of the water. Using sea urchins, they showed that specimens that had been allowed to decay slightly in warm seawater for 2 days fell apart six times faster than those that were not allowed to decay. They found that the longer specimens were allowed to decay, the faster they broke up. The difference between decay in aerobic (oxygen-rich) versus anaerobic (oxygen-poor) settings was not significant, but the temperature of the water was important. The colder the water, the slower the decay, and the longer the sea urchin shells survived tumbling.

How have these durability biases changed through time? Do they distort the fossil record so that comparisons of Paleozoic faunas and Cenozoic shelly faunas are inappropriate? Behrensmeier et al. (2005) looked at the 450 most frequently occurring genera in the Paleobiology Data Base (www.pbdb.org). They found that there was no clear bias over time introduced by shell durability, so that the samples over time should reflect biological and not taphonomic processes. Kosnik et al. (2011) looked at the shell durability data in the Paleobiology Data Base for 48 time intervals, and found that there was no net change in shell durability through time comparing the Paleozoic with the Mesozoic or Cenozoic faunas of bivalves, brachiopods, or gastropods.

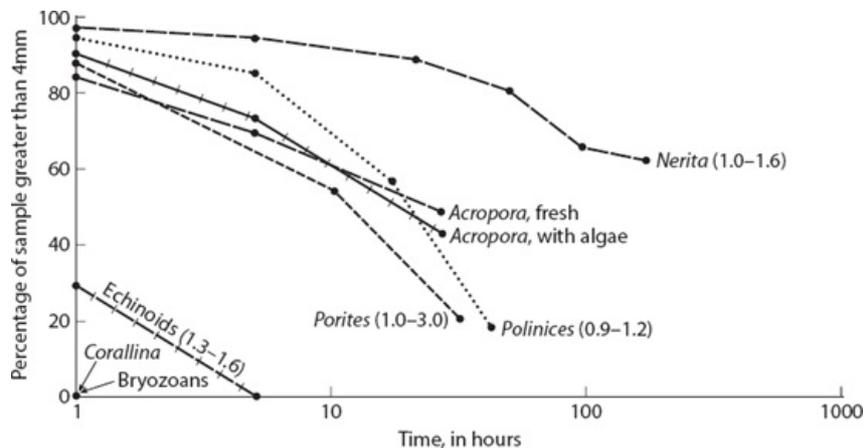


FIGURE 1.12 Tumbling experiments simulate the breakdown of various shells and skeletons and show which are the most delicate and which are the most resistant to the processes of mechanical abrasion. (Modified from Chave, 1964.)

Similar studies have been performed for terrestrial environments (Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Korth, 1979; Hanson, 1980; Shipman, 1981). A classic study by Voorhies (1969) took a series of recent (not fossil) mammal bones and tumbled them in a flume to simulate the processes that occur in a stream. The bones clustered into three well-defined groups (now known as *Voorhies groups*) of increasing durability. The least durable were thin, delicate, elongate Group I bones, such as ribs, vertebrae, and the breastbone (table 1.1). Slightly more durable were shoulder blades and toe bones. Group II consisted of thicker and less delicate bones, such as most of the limb bones and parts of the hip. The most durable elements (Group III) were the skull and jaws, which are dense and heavily sutured together. Even more durable are the individual teeth, which are coated in enamel, the hardest substance in the skeleton. Not surprisingly, most mammal fossils consist of teeth and jaws or less commonly skulls. Limb bones for fossil mammals are found less often, and identifiable ribs and vertebrae are so seldom preserved in association with diagnostic skull or tooth material that they are seldom even collected or described.

In summary, the *shape*, *density*, and *thickness* of the bone or shell are the most important factors in determining its survival under mechanical transport of waves, storms, or river currents.

Diagenesis and Discovery

After burial, a variety of diagenetic changes in the rock (especially metamorphism) can easily destroy the shells and prevent their preservation. As discussed earlier, aragonitic fossils are much more prone to dissolution than calcitic fossils, so fossils made primarily of aragonite are discriminated against in the fossil record. For example, there are a number of calcareous plankton in the fossil record, including the foraminifera, the ostracodes, and a group of tiny aragonitic planktonic snails known as *pteropods*. All three groups can be very abundant in tropical surface waters, but as they die and sink to the bottom, the pteropods dissolve first, because they are made of aragonite not calcite. Many calcareous oozes on the seafloor are not a good reflection of the original plankton in the surface waters, because the pteropods have been selectively dissolved away. Cherns and Wright (2009) found that this bias against aragonitic fossils also has an effect on long-term comparisons of diversity over time. For example, in chapter 7, we will discuss the evidence for a brachiopod-dominated “Paleozoic fauna” that forms the largest percentage of shells in most Ordovician through Permian shallow marine rocks. However, Cherns and Wright argue that molluscs (especially bivalves) were originally much more abundant in Paleozoic rocks than their fossil record suggests, but that selective dissolution of mostly aragonitic molluscs has weeded them out compared with the much more dissolution-resistant calcitic brachiopods, bryozoans, and corals that dominate the “Paleozoic fauna.”

TABLE 1.1 Durability of the bones in a typical mammalian skeleton.

<i>Group I: Immediately removed by low-velocity currents; high surface area/volume ratio</i>	
Ribs	
Vertebrae	
Hip bone	
Breastbone	
<i>(slightly more durable below)</i>	
Shoulder blade	
Finger bones	
<i>Group II: Removed gradually by moderate currents; low surface area/volume ratio</i>	
Thigh bone	
Shin bone	

Upper and lower arm bones

Ankle and wrist bones

Some hip bones

Group III: Lag deposit, moved only by high-velocity currents; low surface area/volume ratio; high density

Lower jaw

Skull

Teeth

After Voorhies (1969).

In another study, Voight (1979) censused a living oyster bank and found over 300 species (mostly soft-bodied worms). Of the shelly invertebrates, 16% (nearly all the snails and many of the bivalves besides oysters) had aragonitic shells. Once these had dissolved, the remaining “oyster community” appears to be of low diversity, but this is a false conclusion—the only species fossilized are those with calcitic shells.

Many apparently unfossiliferous rocks probably had fossils at one time, but diagenesis has removed them. This is usually hard to document, but McCarthy (1977) described a Permian beach sand that had no apparent fossils until he examined scattered concretions. Inside the concretions were abundant fossils, showing the original texture of the rock before groundwater flushed through to dissolve everything not protected by a concretion.

The diagenetic history of a fossiliferous deposit can be very complex. The Miocene Leitha Limestone of southern Austria (Dullo, 1983) has been subdivided into several biofacies based on relative abundance of molluscs, corals, red algae, bryozoans, and foraminifera. However, a closer examination shows that these relative abundances are largely a diagenetic artifact rather than original ecological abundances. Calcitic molluscs such as oysters and scallops, are well preserved in all facies, so they dominate the heavily dissolved facies. Aragonitic molluscs are preserved only in basinal, muddy facies. Aragonitic fossils represented by molds, or replaced by calcite, are found in chalk and well-cemented limestone facies. Aragonitic fossils are completely absent from carbonate sand facies. In this case, the degree of exposure to groundwaters and marine waters is more important than the original community composition.

In summary, the *original composition* and *groundwater chemistry* are the most important factors in determining whether diagenetic changes are likely to alter or dissolve a fossil.

Finally, only a small portion of all the fossiliferous rocks in the world happen to be exposed during just the last few centuries, when people began to collect them. Even a smaller proportion of those outcrops are ever seen by a qualified collector before the fossil erodes out and is destroyed. Thus, the chances of a given animal having the extraordinary luck of being preserved and collected by a paleontologist are extraordinarily small.

Taphonomic research has come a long way since the pioneering studies of the 1960s and 1970s. Paleontologists can no longer afford to naïvely take the fossil record at face value, but must always keep in mind the taphonomic “noise” that may obscure the original biological “signal.” However, not all taphonomic processes are negative. Applied properly, taphonomic information can add to our understanding of the fossil record, and in many cases, we can appreciate dimensions of the past that would otherwise have escaped our notice (see Behrensmeier and Kidwell [1985, 1993] for a review of taphonomic processes and their important positive implications).

WHAT FACTORS ARE REQUIRED FOR EXTRAORDINARY PRESERVATION?

The processes outlined above account for most fossilization, and what we know of the living organism is usually quite incomplete. However, there are extraordinary fossil deposits around the world that preserve soft tissues and sometimes even skin texture and color patterns, giving us a much more complete picture. These are known as **Lagerstätten** (the German means, literally, a “storage place,” but it was long used as an old German mining term for “mother lode”); the singular form is **Lagerstätte**. These deposits have produced some of the most important fossils known. Some of them are so famous that they form an “honor roll” that most paleontologists know by heart (see [table 1.2](#) for a complete list). These are discussed in the sections that follow.

The Middle Cambrian Burgess Shale, British Columbia

In recent years, the most celebrated of all the *Lagerstätten* is the Middle Cambrian Burgess Shale, from the Canadian Rockies in Yoho National Park, British Columbia. A few quarries high on the slopes of Mount Field have produced over 65,000 specimens of mostly soft-bodied animals, representing at least 93 species. Most are preserved as flat impressions on the shales, although the trilobites are preserved with their calcified skeletons as well ([fig. 1.13](#)). These organisms were apparently transported by submarine landslides from a nearby shallow carbonate bank into these anoxic, deepwater shales, where they were abruptly buried in fine mud and not allowed to decay.

What is extraordinary about the Burgess Shale is not just the preservation of typical Cambrian fossils, such as trilobites, but the great number of unique and bizarre soft-bodied animals about which we would otherwise never know. Although the majority can be assigned to existing phyla, many are clearly unique “evolutionary experiments” that belong to no living phylum. In his book *Wonderful Life*, Gould (1989) argues that this “window in time” of the Burgess Shale shows that there were many experimental phyla during the Early Cambrian radiation that did not survive even to the later Paleozoic. Contrary to the long-held expectation that everything in the Cambrian is simple, primitive, and ancestral to living groups, the Burgess Shale shows that there was a great deal of experimentation in unusual body plans during the Cambrian, most of which did not survive.

The Burgess Shale is not unique in this regard. *Lagerstätten* from Chengjiang, Yunnan Province, China, and Sirius Passet, Greenland, have produced similar forms, showing that the explosion of experimental forms took place around the world in the Cambrian.

The Upper Jurassic Solnhofen Limestone, Southern Germany

This deposit was first quarried, because it yields extremely fine-grained slabs of limestone that were perfect for the acid-etching process to produce lithographic printing plates. Apparently, these limestones were produced when fine lime mud washed from the ocean into a shallow stagnant lagoon, which was low in organic productivity (so the rocks are not black with organic matter, but pale buff to white in color) and completely hostile to all forms of life on the bottom. As animals died and sank to the bottom, there were no scavengers or decomposers to decay them, no currents to break them up, and apparently they were rapidly buried as storms brought in new layers of lime mud. There are more than 600 fossil species preserved in the Solnhofen Limestone, including over 180 species of insects, and many marine arthropods (especially crustaceans), such as a well-known specimen of the horseshoe crab *Mesolimulus* preserved at the end of its final trail (fig. 19.1). The most striking specimens are the terrestrial vertebrates, including numerous pterodactyls (fig. 1.14A), which sometimes preserve their body outline and wing membrane, and all 11 known specimens of the earliest bird, *Archaeopteryx*, complete with feather impressions (fig. 5.1). These specimens are important as the “missing link” between birds and dinosaurs, especially because the first specimen was found just 2 years after Darwin’s *On the Origin of Species* was published, providing dramatic evidence for his theory.

TABLE 1.2 Famous Lagerstätten.

<u>Pre-Cambrian</u>		
Bitter Springs	1000–850 Ma	South Australia
Ediacara Hills	630–542 Ma	South Australia
Doushantuo Formation	600–555 Ma	Guizhou Province, China
Mistaken Point	565 Ma	Newfoundland, Canada
<u>Cambrian</u>		
Maotianshan Shales (Chengjiang)	525 Ma	Yunnan Province, China
Sirius Passet	518 Ma	Greenland
Emu Bay Shale	517 Ma	South Australia
Kaili Formation	513–501 Ma	Guizhou province, south-west China
Wheeler Shale (House Range)	507 Ma	Western Utah, United States
Burgess Shale	505 Ma	British Columbia, Canada
Kinneulle Orsten and Alum Shale	500 Ma	Sweden
Öland Orste and Alum Shale	500 Ma	Sweden
<u>Ordovician</u>		
Fezouata Formation	c. 485 Ma	Draa Valley, Morocco
Beecher’s Trilobite Bed	445 Ma	New York, United States
Soom Shale	435 Ma	South Africa
<u>Silurian</u>		
Ludlow bonebed	420 Ma	England
<u>Devonian</u>		
Rhynie Chert	400 Ma	Scotland
Hunsrück Slates	390 Ma	Rheinland-Pfalz, Germany
Miguasha National Park	370 Ma	Québec, Canada
Canowindra, New South Wales	360 Ma	Australia
Gogo Formation	350 Ma	Western Australia
<u>Carboniferous</u>		
Bear Gulch Limestone	320 Ma	Montana, United States
Joggins Fossil Cliffs	315 Ma	Nova Scotia, Canada
Mazon Creek	300 Ma	Illinois, United States
Hamilton Quarry	295 Ma	Kansas, United States
<u>Triassic</u>		
Karatau	230 Ma	Kazakhstan
<u>Jurassic</u>		
Holzmaden/Posidonia Shale	180 Ma	Württemberg, Germany
La Voulte-sur-Rhône	160 Ma	Ardèche, France
Solnhofen Limestone	145 Ma	Bavaria, Germany
<u>Cretaceous</u>		
Yixian Formation	c. 125–121 Ma	Liaoning, China

Las Hoyas	c. 125 Ma (Barremian)	Cuenca, Spain
Crato Formation	c. 117 Ma (Aptian)	Northeast Brazil
Xiagou Formation	c. 110 Ma	Gansu, China
Santana Formation	108–92 Ma	Brazil
Smoky Hill Chalk	87–82 Ma	Kansas and Nebraska, United States
Ingersoll Shale	85 Ma	Alabama, United States
Auca Mahuevo	80 Ma	Patagonia, Argentina
Zhucheng	65 Ma	Shandong, China
<u>Eocene</u>		
Green River Formation	50 Ma	Colorado/Utah/Wyoming, United States
Monte Bolca	49 Ma	Italy
Messel Oil Shale	49 Ma	Hessen, Germany
<u>Oligocene–Miocene</u>		
Dominican amber	30–10 Ma	Dominican Republic
Riversleigh	25–15 Ma	Queensland, Australia
<u>Miocene</u>		
Clarkia fossil beds	20–17 Ma	Idaho, United States
Ashfall fossil beds	10 Ma	Nebraska, United States
<u>Pleistocene</u>		
The Mammoth Site	26,000 years BP	South Dakota, United States
Rancho La Brea Tar Pits	35,000–9,000 years BP	California, United States

Ma, millions of years ago; BP, before present.

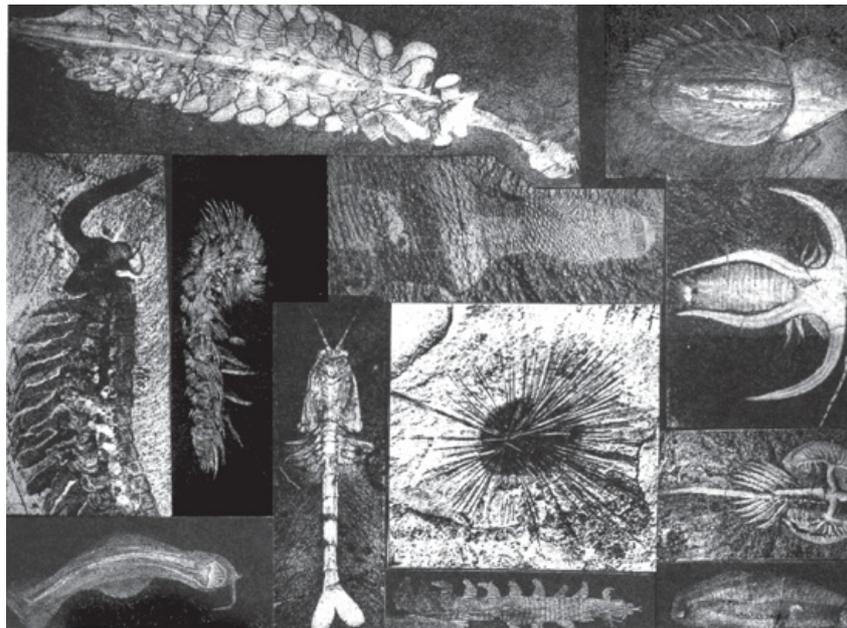


FIGURE 1.13 Soft-bodied impressions from the Middle Cambrian Burgess Shale showing the exquisite detail of the preservation of the appendages and even the bristles of these strange creatures. (Photo courtesy of the Smithsonian Institution.)

The Pennsylvanian Mazon Creek Beds, Northeastern Illinois

Exposures of the Middle Pennsylvanian Francis Creek Shale of the Carbondale Formation in the Mazon Creek area of northeastern Illinois yield nodules of siderite (iron carbonate) that, when split open, reveal soft-bodied organisms preserved in exquisite detail (fig.1.14B). Over 350 species of plants (the most diverse fossil flora known in North America), 140 species of insects, and over 100 additional taxa, including bivalves, jellyfish, worms, sea cucumbers, centipedes, millipedes, scorpions, spiders, crustaceans, fish, and amphibians are known. In addition, there are soft-bodied enigmas like the “Tully monster” (a bizarre worm-like creature) that cannot be assigned to any known phylum.

The absence of normal marine taxa and the sedimentology suggest these fossils were quickly buried at the mouth of an estuary–delta complex when sediment-laden floods of freshwater rapidly buried everything on the muddy bottom. The rotting tissues changed the chemistry of the mudstone, such that iron carbonate could precipitate and nucleate around the organism, forming a concretion. These concretions must have formed very early, for many of the fossils are undistorted, even though the surrounding shales have undergone much compaction.

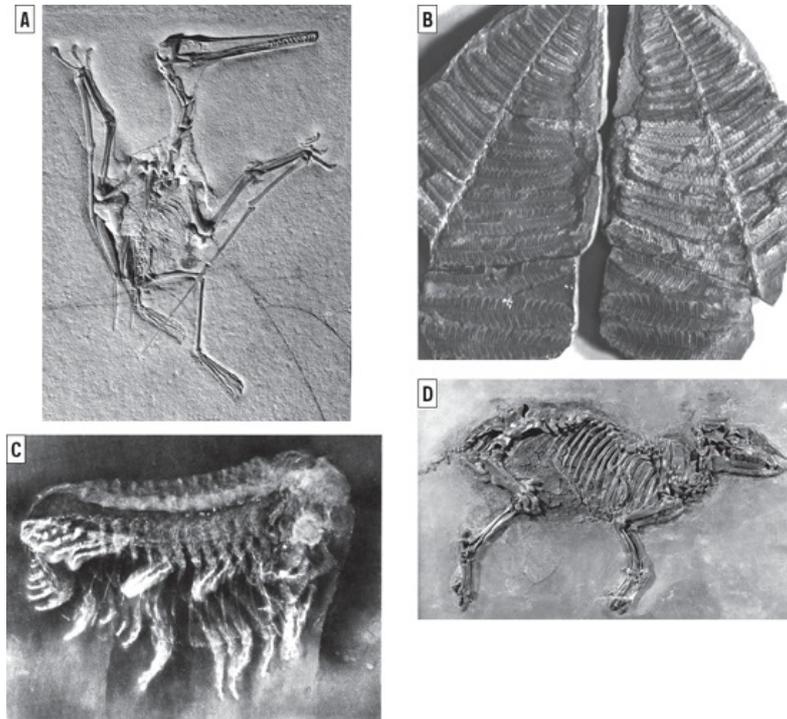


FIGURE 1.14 Fossils from some famous *Lagerstätten*. (A) *Pterodactylus* specimen from the Upper Jurassic Solnhofen Limestone of Germany. (Reprinted by permission of P. Wellnhofer, Bayerisches Staatssammlung, München.) (B) Typical siderite nodule from the Pennsylvanian Mazon Creek beds of Illinois, split in half to reveal both sides of a delicately preserved fern fossil. (Photo by the author.) (C) This Devonian trilobite from the Hunsrück Shale of Germany has been x-rayed to show the soft appendages and gills. (Photo courtesy of W. Stürme.) (D) Complete articulated specimen of the horse-like palaeothere *Propalaeotherium* from the Eocene lake deposits of Messel, Germany. Not only is every bone in place, but the body outline and even the fine structure of the vegetation in the stomach are preserved. (Photo courtesy of Dr. J. L. Franzen, Forschungsinstitut Senckenberg.)

Other *Lagerstätten*

In addition to these classic localities, there are the Lower Devonian **Hunsrück Shale** (*Hunsrückschiefer*) of western Germany, which produced over 400 species of animals with soft parts preserved, including segmented worms and trilobites (fig. 1.14C) with all their soft limbs, gills, and antennae. The Middle Jurassic *Posidonienschiefer* of **Holzmaden**, southern Germany, yielded over 100 species of Jurassic marine life, including squids and ichthyosaurs with their body outlines preserved as a dark film (fig. 1.9B); one ichthyosaur was preserved in the process of giving birth (fig. 8.10A). Both of these deposits are classic black shales, formed in deep, stagnant water, where there were few currents or scavengers to break up the carcasses.

The middle Eocene deposit at **Messel**, in western Germany, is an oil shale deposit formed at the bottom of a stagnant lake (fig. 1.14D). Many different plants and animals (especially insects, fish, frogs, turtles, lizards, snakes, crocodiles, birds, and about 35 species of primitive mammals) are preserved with impressions of the soft tissue and body outlines. There are also extraordinary examples of preservation of cell walls of plants, hair from mammals, scales from the wings of moths, color patterns on many of the insects, and the stomach contents of many of the animals.

From all these examples, several general trends emerge. The best fossilization occurs when there is rapid burial and anoxic conditions to prevent scavenging, no reworking currents, and little or no diagenetic alteration to destroy the fossils.

HOW GOOD IS THE FOSSIL RECORD?

To those who believe that the geological record is in any degree perfect will undoubtedly at once reject the theory [of evolution]. For my part, following out Lyell's metaphor, I look at the geological record as a history of the world imperfectly kept, and written in a changing dialect; of this history, we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines.

—Charles Darwin, *On the Origin of Species*, 1859

All of the descriptive and anecdotal evidence we have just reviewed underlines the incompleteness of the fossil record. Can we also get a quantitative estimate of its quality? Can we answer in numerical terms the question: How good is the fossil record?

Let us start with some simple estimates. We have already estimated that there are 1.5 million described species, or as many as 4.5 to 10 million described and undescribed species of organisms alive on Earth today. How many species are known as fossils? It turns out that there are only about 250,000 described species of

fossil plants and animals presently known, or only 5% of the total for species living today. But the present is only one moment in geologic time. If we multiply the present diversity by the 600 million years (m.y.) that multicellular life has existed on this planet, the estimate is much worse. No matter how one does this calculation, it is clear that the quarter of a million species known as fossils represents only a tiny fraction of a percent of all species that have ever lived.

But all is not lost. Almost half of the 1.5 million described species are insects, which have a poor fossil record. Let us just focus on nine well-skeletonized phyla of marine invertebrates and see if we come up with better estimates (table 1.3). These nine phyla are the Protista, Archaeocyatha, Porifera, Cnidaria, Bryozoa, Brachiopoda, Mollusca, Echinodermata, and Arthropoda (excluding insects). In these groups, there are about 150,000 living species, but more than 180,000 fossil species (Valentine, 1970; Raup, 1976a). To translate these numbers into completeness estimates, we need to know the turnover rate of species and the number of coexisting species through time. Different values have been used for each of these variables, but the results of the calculations are remarkably similar. Durham (1967b) estimated that about 2.3% of all the species in these nine phyla were fossilized. Valentine (1970) gave estimates that ranged from 4.5% to 13.6%. No matter which method we use, we must conclude that 85% to 97% of all the species in these nine well-skeletonized phyla that have ever lived have never been fossilized.

TABLE 1.3 Proportion of living taxa with a fossil record.

<i>Group</i>		<i>Percent</i>
Sponges	Family	48
Corals	Family	32
Polychaete worms	Family	35
Malacostracan crustaceans	Family	19
Ostracode crustaceans	Family	82
	Genus	42
Bryozoans	Family	74
Brachiopods	Family	100
	Genus	77
Crinoids	Family	50
Asterozoans (sea stars)	Family	57
	Genus	5
Echinoids	Family	89
Bivalves	Family	95
	Genus	5
Gastropods	Family	59
Cephalopods	Family	20
Cartilaginous fishes (sharks, rays)	Family	95
Bony fishes	Family	62
Arachnids (spiders, scorpions, and their kin)	Genus	2
	Species	<1

This is a very sobering estimate. It forces us to step back and reassess the limitations of almost any study based on fossil data. However, there is another consideration to keep in mind: the quality of the record depends on the level of detail we require. For a census of all the phyla or classes of invertebrates in a given sample, it would not be hard to get a complete sample. Obtaining every species is much harder. The reason for this is simple: a higher taxon such as a phylum or class contains many different genera and species. If we obtain one species in each given phylum or class in a sample, we have a complete sample of phyla or classes with only a few specimens. But we may need huge samples to get every species, or even every family or genus that might have lived in a given time and place (see box 1.1). Ideally, we would like to use species as our unit for most analyses, because the species is the only “real” natural taxonomic category that the organisms themselves recognize (see chapter 3). But given the much greater difficulty in sampling all the species versus genera or families in a given locality, this is not always possible.

Other approaches have suggested that the quality of our paleontological data set is not quite this bad, at least for the problems that paleontologists want to address. Benton et al. (2000) tried a novel approach: they compared the phylogeny (family trees) of many different groups of animals with their actual appearance in the fossil record to determine how many gaps in the phylogeny trees were found at different time intervals. They calculated the **stratigraphic consistency index** (SCI), which directly compares the phylogeny of a group of animals with its stratigraphic order of appearance to determine how much the first appearance of each group matches its predicted branching points on the family tree. They also looked the **relative completeness index** (RCI), the actual amount of time between the predicted first appearance of a group and its actual appearance, and the **gap excess ratio** (GER), a modification of the RCI that compares the actual proportion of missing fossil ranges (“ghost ranges”) with the minimum and maximum ghost ranges when the phylogeny is modified. Benton et al. (2000) found that there was no net change in the SCI, GER, or SCI/GER ratio from the Paleozoic to the Recent in over 1000 published phylogenies of different groups of animals. In other words, the record is equally good (or equally bad) through the past 540 m.y., so comparisons between time intervals are not affected by

biases such as the fact that Cambrian and other old rocks and localities are much rarer and their total number of fossils are also rarer.

Benton and Storrs (1994) also did a study in which they showed that the quality of the fossil record is improving rapidly, as more localities are found and more and more fossils are studied and published. Using the same method of comparing the phylogeny of 74 groups of vertebrates with their stratigraphic record, they showed that the RCI has improved remarkably over the years. In one case study, they compared the level of paleontological knowledge as it was in 1967 with the level in 1993, and found about a 5% improvement in only 26 years. Of course, this situation varies from group to group. In some groups of fossils, no recent update has been done in decades or more (such as North American camels or pronghorns) despite huge new collections of fossils, so no attempt to draw conclusions from the existing record would be very meaningful. In other cases, there are complete updates of entire families (e.g., Prothero [2005] on all North American rhinoceroses), so that data set is very current and any conclusions based upon it would be considered reliable.

Box 1.1. Rarefaction Analysis

We have mentioned the problem with sampling and the biases of small sample sizes. How big does a sample need to be before we can make assertions based upon it? This problem has been discussed by ecologists and field biologists since 1968, when ecologist Howard Sanders was trying to determine whether his samples of diversity of marine organisms was sufficient to make comparisons. This method, known as **rarefaction**, is now widely used not only in ecology but also in paleontology as a way to determine whether two samples can be reliably compared.

For example, there are standard plots in biology (fig. 1.15) that help estimate how many specimens one must have in the sample to achieve a specific level of completeness of all the taxa represented. The completeness varies with the taxonomic level. For example, in the curves in fig. 1.15, one needs roughly 1000 specimens to obtain 100% of all the classes of animals that live in a given area, but many thousands to obtain all the orders or families. When the sample approaches 3000 specimens, even the species are nearly completely sampled. Conversely, if one has only 1000 specimens, these curves suggest that you have about 100% of the classes, 80% of the orders, 70% of the families, and about 60% of the genera and species that are actually present in a given place and time.

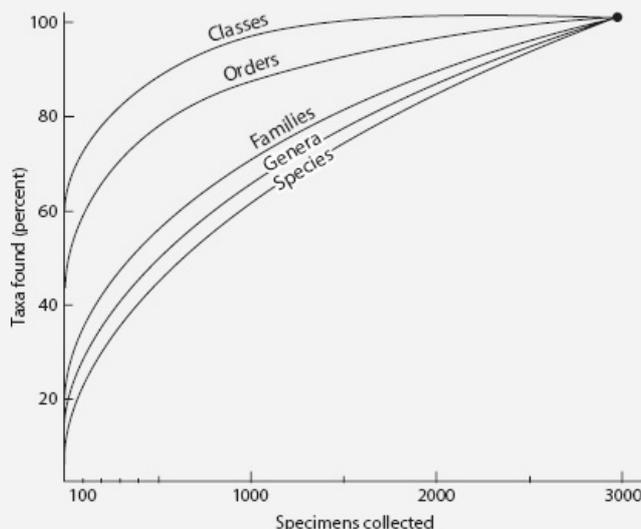


FIGURE 1.15 Rarefaction curves for molluscan fossils from a Miocene sample in Denmark (based on data from Sorgenfrei, 1958). The point in the upper right represents the actual sample of 2954 specimens. Each curve is an estimate of how many taxa of different ranks would have been found had the sample been smaller.

For fossil samples, rarefaction analysis allows a paleontologist to compare two samples of unequal size and estimate whether their differences are real or due to sampling. In fig. 1.16, there are different samples of land mammal fossil assemblages of different sizes. The samples from the earliest Eocene (G, Graybullian) and late early Eocene (LG, Lostcabinian–Gardnerbuttean) are both gigantic, with tens of thousands of specimens in the collections. Nonetheless, their curves have very different slopes, suggesting that the true diversity of G is much lower than that of LG. The sample from the middle Eocene (UD, Uintan–Duchesnean), on the other hand, is much smaller, with fewer than 1000 known specimens (only a few hundred specimens are known from the Duchesnean, in particular). Yet despite the small number of specimens, the rarefaction curve suggests that the true diversity is very high, almost as high as LG. Finally, the late Eocene–early Oligocene sample (CO, Chadronian–Orellan) is by far the largest of all, yet its rarefaction curve shows that the diversity is quite low, despite all the excellent specimens from places like the Big Badlands of South Dakota.

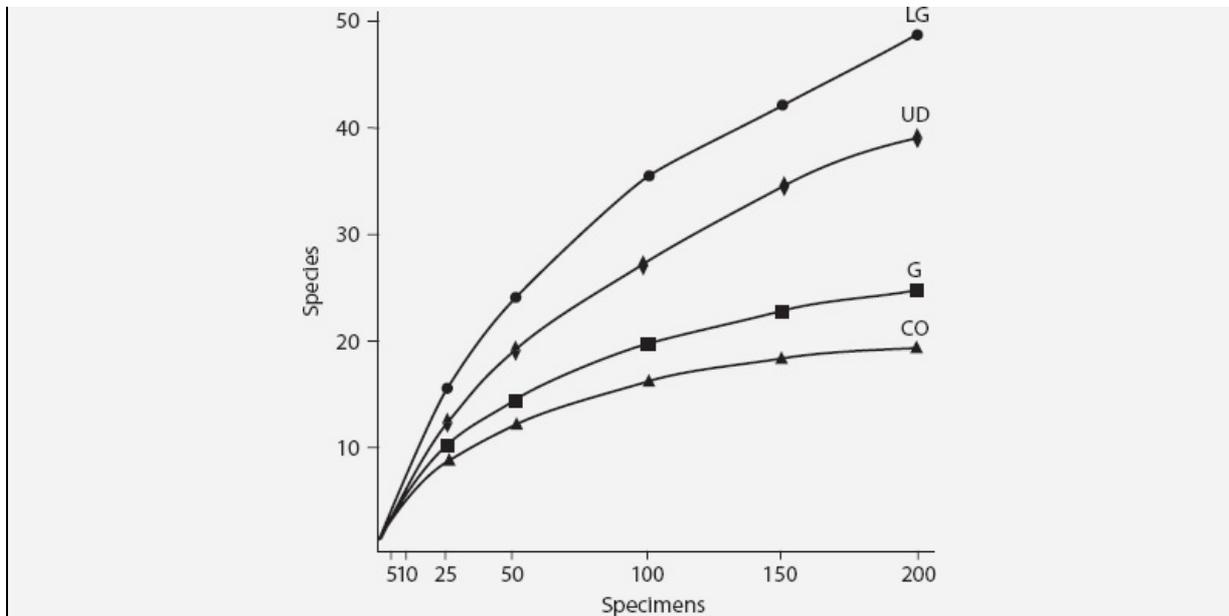


FIGURE 1.16 Rarefaction curves for North American mammals of the Eocene and Oligocene. (After Stucky, 1992.) See text for discussion.

Although the mathematics of rarefaction analysis is not very complicated, it is not necessary to do a lot of calculations on paper any more. A simple rarefaction program is available at <http://www2.biology.ualberta.ca/jbrzusto/rarefact.php>, so any paleontologist can quickly convert diversity data for a relative sample size and determine whether the differences in number of species in each sample is real or an artifact of small or large samples.

We should point out that this issue of data quality is not a problem unique to paleontology. All areas of science have issues with incomplete or missing data, whether they are conscious of it or not. Many fields do not spend much time thinking about this limitation, while paleontologists have a whole subfield, taphonomy, devoted to its study. Even if a given field of science does not think about its data limitations, researchers have learned by experience which data are the most complete and informative and have focused their explanations on the best data they have.

In short, if we want to conduct large-scale studies of evolutionary trends, we must concentrate on the higher taxonomic levels (kingdom, phyla, classes, and orders); we cannot expect to work at the species level. But in local problems, we can often select faunas with the best possible preservation, which might allow us to trust the species-level data.

CONCLUSIONS

The answer to the question “How good is the fossil record?” is a complex one. For certain types of studies, it is excellent; for others, it is useless. A good paleontologist knows when the data are worth pursuing and when they are so bad that any analysis is “garbage in, garbage out.” In the following chapters, we will review some of the excellent research that has taken advantage of the strengths of the fossil record. Naturally, we do not feature the many studies (mostly never published) that did not take these limitations into account.

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