

Chapter 1

THE NATURE OF THE FOSSIL RECORD

1.1 NATURE AND SCOPE OF PALEONTOLOGY

- *Fossils are mainly found in sedimentary rocks, and so where we find fossils is largely a matter of where we find such rocks. Over 30 years ago, paleontologists documented a simple correspondence between the amount of preserved sediment and the number of fossil species known from a given period of geologic time (Figure 1.1). This raises the obvious (and still unanswered) question: How well do changes in biological diversity that we see in the fossil record reflect the true course of diversity in the history of life?*
- *The chances that an organism will be fossilized after it dies are quite small. This would lead us to expect that the full roster of species living in a community today will not ultimately be represented in the fossil record. Nonetheless, if we want to build a complete list of the species living in a given area, it is often possible to do so more effectively by sampling dead skeletal remains from the unconsolidated sediment than by sampling live individuals [SEE SECTION 1.2]. Why should this be?*
- *By studying individual species in great detail, paleontologists have found that many species show scarcely any evolutionary change over millions of years. If this is so, how can there be major evolutionary trends in the history of life—for example, toward greater body size, higher complexity, more efficient feeding, or increased intelligence [SEE SECTION 7.4]?*

These are but a few of the questions addressed by **paleontology**, which is the study of ancient life in its broadest sense. While this definition is clear enough, it does not convey the excitement that currently envelops the field. In fact, it can be said fairly that paleontology is in

the midst of a renaissance, spurred on by a new generation of analytical techniques and approaches that unlock the fossil record for application to geological, biological, and even astronomical questions—which may surprise some students—related to the history, current state, and future of life on the planet.

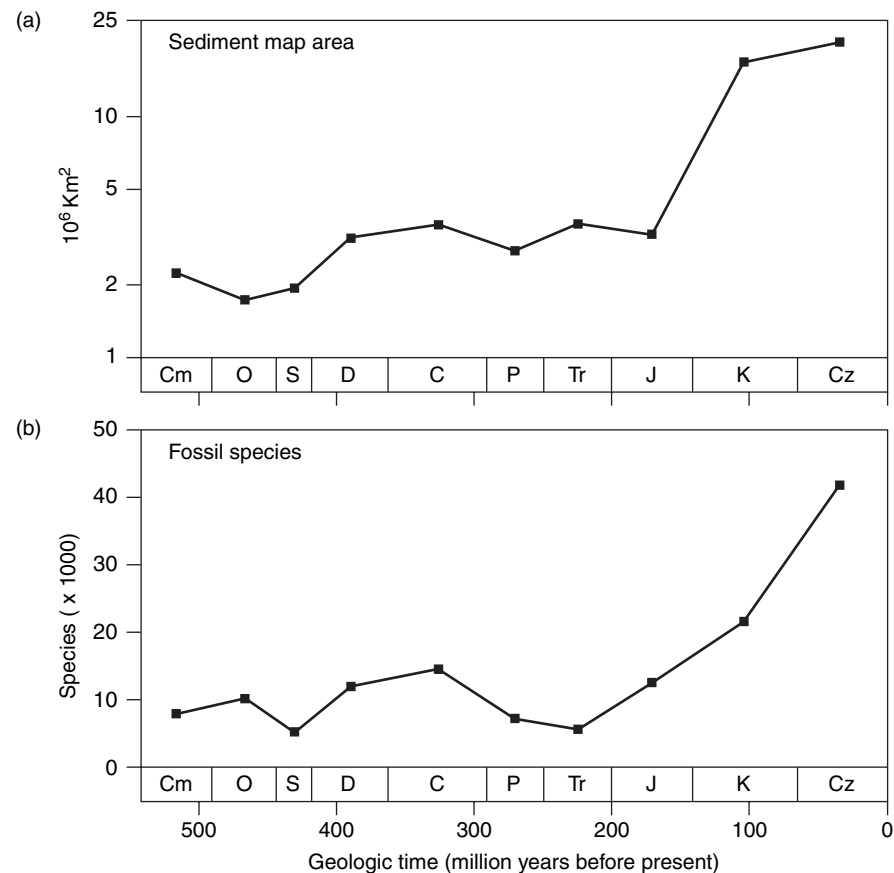
The data of paleontology come from the form, chemistry, and spatial and temporal distribution of fossils. The term **fossil** (from the Latin *fodere*, to dig) was once used to refer to nearly any object dug up from the ground, but now refers more specifically to remains of past life. Fossils are mechanically or chemically extracted from rocks or unconsolidated sediments that crop out naturally at the earth's surface or are exposed by activities such as road building and mining. Historically, the fossil record has been most thoroughly studied near major population centers in the developed world. Following initial reconnaissance surveys, however, increasing efforts are being made to sample from remote regions such as Antarctica.

The relationship between observed diversity and preserved sediment just mentioned reflects the more general issue of how the imperfections of the fossil record affect our ability to study the life of the past. A central theme of this book is that the nature of the fossil record must be taken into consideration at all times but that its deficiencies can be rigorously addressed. One of our main goals is to help students interpret the data of the fossil record, often with the help of models and observations on how it forms, while avoiding two pitfalls. The first is the assumption, often tacit, that the fossil record is so complete that it can always be taken at face value. The

FIGURE 1.1 Sedimentary rocks and fossil diversity through geologic time.*

(a) The outcrop area of sedimentary rock as measured from geological maps for periods of time in the Phanerozoic. (These data are plotted on a logarithmic scale, which is used to emphasize proportional variation among numbers. A unit difference on such a scale represents a constant ratio between numbers; for example, the difference between 1 and 2 is the same as that between 5 and 10.) (b) An estimate of the numbers of invertebrate species that were discovered and named between 1900 and 1975. Pleistocene and Holocene data are ignored in both figures. All data were compiled from global sampling. Periods of time with more sedimentary rock tend to have more fossil species as well. (Data are from Raup, 1976a, b)

* Please see the geologic timescale on the inside front cover of this book.



second pitfall, in effect the opposite of the first, is the assumption that the fossil record is so biased or incomplete that it is of little scientific use.

In fact, incompleteness often leads to very specific predictions about the distortion of patterns in the fossil record, and these predictions can be used to advantage. To take a simple example, calcite is a form of calcium carbonate that is more stable than an alternative form, aragonite [SEE SECTION 1.2]. Most **BRACHIOPODS**¹ have calcitic shells, whereas both aragonite and calcite are common in **BIVALVE MOLLUSCS**. We might therefore expect bivalves to have a lower preservation potential and to be more severely underrepresented in the fossil record. During the Mesozoic and Cenozoic Eras, however, the number of fossil bivalve species increased greatly relative to that of brachiopods. This observation goes against the prediction of the postulated bias and is therefore not a result of it. We can trust that bivalves really have diversified more than brachiopods over the past 250 million years.

¹ Please see the inside back cover for a summary of the paleontologically important groups of organisms.

Considering the incompleteness of the fossil record naturally leads to the question of how to interpret the absence of a species or a larger biologic group in the record of a particular time and place. Given the rarity of preservation, absence from the record does not necessarily imply that the organisms in question did not live there. One way to determine whether an absence is true or preservational is to use the notion of **taphonomic control**. (**Taphonomy**, as we will discuss below, is the study of fossilization processes.) If one species is not found but a preservationally similar species—the taphonomic control—is found, then we know the necessary conditions for preservation were present. In such a case, the absence of the first species is more likely to reflect a true absence than if the taphonomic control had not been found.

1.2 FOSSIL PRESERVATION

One of the remarkable aspects of the fossil record is the variety of ways in which a once-living organism can be preserved as a fossil. Intuition alone suggests that the possession of skeletal material (**hard parts**) should enhance the likelihood of preservation, and this is generally the

case. However, the preservation of hard parts is not straightforward. Skeletal material typically undergoes mechanical and chemical alteration following the death of the organism and the microbial decay of soft tissues (**soft parts**). Most mineralized skeletons have an associated **organic matrix** that is subject to rapid degradation; this may compromise the post-mortem durability of the skeleton. Moreover, soft parts can be preserved in the fossil record under unusual circumstances. Combining experiment with observation, paleontologists have come to understand many of the intricacies of fossil preservation and how they relate to the questions we treat in this book.

General Considerations

Post-Mortem Degradation Environments in which life can exist are generally teeming with organisms. Death is quickly followed by scavenging, decay of organic tissue, and use of hard parts as substrates by other organisms. Thus, a number of biological processes reduce the chances of fossilization, and removal to an area of lower biological activity, by transport or burial, can enhance preservation. Nonetheless, biological activity can

actually improve the prospects of preservation. Organisms that encrust shelly material may shield the shells from dissolution. Experimental work also shows that colonization by bacteria shortly after death plays an important role in the preservation of soft parts by changing local water chemistry in a way that favors mineral precipitation. Finally, organisms, such as certain shrimp, that continuously move sediment through their burrows in order to process it for food may significantly accelerate burial of skeletal material (see Figure 9.13).

Physical factors of degradation include wind and freeze-thaw cycles in subaerial environments, and current and wave activity in subaqueous environments. The erosive force of wind comes primarily from the sediment suspended in the air, whereas in the water, the energy of the moving water itself is important in addition to the effect of erosive sediment. As we will see below, field observations and experiments intended to simulate physical transport show that all but the most robust skeletons can be quickly degraded when they are moved by water currents.

Although many materials are known to be biologically produced (Table 1.1), the most important constituents are organic compounds, carbonates, phosphates,

TABLE 1.1

Paleontologically Important Groups of Organisms and the Principal Inorganic and Organic Components They Produce (● indicates a major component and ○ a minor component)

Group	Inorganic				Organic				
	Carbonates	Phosphates	Silica	Iron Oxides	Chitin	Cellulose	Lignin	Collagen	Keratin
Prokaryotes	●	○		○		○			
Algae	●		○		○	●			
Plants	○		○	○		●	●		
Unicellular eukaryotes	●		●	●	○	○			
Fungi	○	○		○	●	●			
Porifera	●		●	○				●	
Cnidaria	●				○			○	
Bryozoa	●	○			●			○	
Brachiopoda	●	●			●			○	
Mollusca	●	○	○	○	○			○	
Annelida	●	●		○	○			●	
Arthropoda	●	●	○	○	●			○	
Echinodermata	●	○	○					●	
Chordata	○	●		○		○		●	●

SOURCE: Towe (1987)

and silica. Organic materials are composed mainly of carbon, hydrogen, nitrogen, and oxygen. They include **chitin** (a major component of **ARTHROPOD** cuticles and **FUNGI**), **cellulose** and other **polysaccharides** (major components of cell walls in **ALGAE** and plants), **lignin** (a constituent of conductive tissue in **VASCULAR PLANTS**), **collagen** (forming much of the connective tissue in animals), and **keratin** (a protein constituent of horns, claws, bills, and feathers). **Carbonates** include calcium carbonate, CaCO_3 , which is secreted by a diverse array of organisms. **Calcite** is thermodynamically the more stable form of CaCO_3 ; **aragonite** is less stable and tends to dissolve or to convert to calcite over time. **Phosphates** include calcium phosphate, one form of which is **apatite**, $\text{Ca}_5(\text{PO}_4, \text{CO}_3)_3(\text{F}, \text{OH}, \text{Cl})$. This class of minerals is important in **VERTEBRATE** teeth and bones, in the shells of some brachiopods, and in the jaw elements of **ANNELIDS**. Hydrous **silica**, or **opal**, $\text{SiO}_2 \cdot \text{H}_2\text{O}$, is less common than carbonates and phosphates, but it is important in such groups as the **SPONGES** and single-celled **DIATOMS** and **RADIOLARIA**.

Basic chemistry dictates the conditions under which biological materials tend to be stable. For example, organic compounds are generally unstable under oxidizing conditions. This fact reflects chemical reaction with oxidants as well as scavenging and other activities of organisms that live in oxygen-rich environments. Thus, the presence of well-preserved organics tells us that conditions were not strongly oxidizing. Carbonates tend not to persist below a **pH** of about 7.8, whereas phosphates and silicates are stable under slightly more acidic conditions.

Consideration of organic preservation naturally leads to the subject of genetic material. **DNA** is not an extremely stable molecule, so most confirmed cases of preserved DNA involve desiccated or frozen organisms less than one million years old. Contamination by other sources of DNA, including microbes and human lab workers, is a major problem, and rigorous tests are required to establish the authenticity of ancient DNA. To take just one example of what can be done with ancient genetic material, DNA from extinct mammoths (*Mammuthus*) has been compared with that of Asian and African elephants (*Elephas* and *Loxodon*). Recent analyses of DNA sequences suggest that the DNA of *Elephas* is more similar to that of *Mammuthus* than it is to *Loxodon*, and that therefore mammoths and Asian elephants are more closely related in an evolutionary sense [SEE SECTION 4.2] than are the living elephants with each

other. There is some uncertainty here, and earlier analyses had suggested a closer affinity between *Mammuthus* and *Loxodon*. Regardless of how this particular case is resolved, the number of reliable instances of ancient DNA is increasing rapidly, and analysis of this material will continue to play an important role in a variety of evolutionary studies.

Biological Traits that Enhance Preservability Considering the major biological, physical, and chemical factors of degradation, we can predict the kinds of organisms and parts of organisms that should stand the best chance of becoming fossilized. Because the organic matrix of skeletal materials often degrades quickly after death, a higher ratio of mineral to organic material tends to enhance preservability. The **TRILOBITE** cuticle has a much higher proportion of calcium carbonate than does the cuticle of **MALACOSTRACAN CRUSTACEANS**. Accordingly, trilobites stand a greater chance of fossilization. Similarly, the dense teeth of vertebrates are generally more durable than their bones.

The number of skeletal elements and how they are joined also influence preservability. Sponges often contain a large number of isolated spicules in an organic matrix, while many **CORALS** consist of a single, robust skeletal element. Corals therefore tend to preserve more readily. The mineral composition is also significant. As mentioned earlier, calcite is a more stable form of calcium carbonate than is aragonite. Thus, aragonitic species are sometimes found with their shells dissolved in the same deposits in which the shells of calcitic species are preserved intact. Organic molecules also differ in their stability. Lignin is less likely to decompose than cellulose, for example. As a result, lignin-rich vascular plants generally are more likely to be preserved than nonvascular plants. The waxy cuticle that covers the surfaces of vascular plants is also resistant to decay.

In addition to structural features of organisms, aspects of their ecology also influence fossilization potential. Perhaps most important is habitat. The land is an area of net sediment erosion while lakes, seas, and parts of river systems are areas of net sediment deposition. For this reason, aquatic organisms stand a better chance of being buried shortly after death and removed from biological activity; terrestrial organisms are most likely to fossilize if they are transported to subaqueous environments. Overall, then, the marine realm has a richer and more complete fossil record than the terrestrial realm. All else being equal, we might also expect species with greater

numerical abundance to have better chances of fossilization. This is not a straightforward expectation, however, because species with more individuals tend to have smaller body size, while larger body size in many cases enhances the chances of at least partial preservation.

Time Averaging Fossil assemblages are generally **time averaged**; that is, they represent an assemblage of skeletal material that has accumulated over some span of time, typically tens to thousands of years but in some cases extending to millions of years. Instantaneous deposits are in fact quite rare. Time averaging results from a number of factors but depends mainly on the rate of production of preservable skeletal material and on the rate of sediment accumulation. For a given rate of skeletal production, a lower rate of sedimentation will allow more generations to be represented in a given thickness of rock, which will therefore be more time averaged. This is complicated by the fact that very low sedimentation rate can lead to long-term exposure and therefore destruction of skeletal material. Sedimentary beds can also become time averaged through **bioturbation**. This is the normal churning and reworking of unconsolidated sediments that occurs as a by-product of such organismic activities as burrowing and ingesting sediment to extract food.

Many living species exhibit a patchy spatial distribution [SEE SECTION 9.3]. Therefore, an instantaneous collection of living individuals from a single locality would not contain all the species living in the larger area which that locality represents. Over time, however, the spatial distributions of species fluctuate as a result of both chance variation in colonization and temporal variation in the distribution of particular habitats. Consequently, a time-averaged sample of fossil organisms from a particular locality may provide a far more complete representation of species that lived in an area than could have been obtained by sampling the living biota over the same lateral extent. This benefit comes at the cost of decreased temporal resolution, however, and in some cases a loss of information about fine-scale spatial patchiness.

The importance of time averaging depends on the timescale of the process we are studying. If we are interested, for example, in reconstructing local communities that lived in the past, a significantly time-averaged assemblage may include species that never lived together. In contrast, evolutionary changes in biologic form often occur over hundreds of thousands to millions of years—spans of time substantially longer than the typical scales

of time averaging. The analysis of such changes, therefore, is barely affected by this process. Much has yet to be learned about the scale of time averaging in different geologic situations, and paleontologists are now attempting to measure time averaging by radiometric dating and other methods that reveal the ages of dead shells [SEE SECTION 10.6].

Modes of Fossilization

Paleontologists have recognized different modes by which individual organisms can become fossilized. These form a spectrum of preservation that ranges from most complete (including preservation of soft parts or easily degraded hard parts such as chitin) to least complete (preservation of only indirect traces of the organism). Preservational modes near the top of the following list are far less common than those near the bottom.

1. *Freezing* (Figure 1.2a). In rare circumstances, ancient organisms, such as woolly mammoths, have been found virtually intact, frozen in permafrost regions of Siberia and elsewhere. These specimens are only a few thousand years old and, thus, may be on the fringes of what we would define as fossils. Their preservation is truly remarkable nonetheless, and they have provided unique opportunities to study the species in question. For example, DNA and gut contents have been extracted from frozen animals.
2. *Preservation in amber* (Figure 1.2b). This is one of the primary means through which **INSECTS** and **SPIDERS** are preserved as fossils. Relatively small organisms sometimes become trapped in highly viscous resin secreted by various trees. When the resin hardens, the trapped organisms are preserved relatively intact in a transparent medium. Incidentally, ancient air bubbles have also been trapped in amber. Geochemists have studied these for clues about the composition of the earth's atmosphere in the past.
3. *Carbonization* (Figure 1.2c). Soft parts of organisms may be preserved as carbon films through **distillation** under heat and pressure, which preferentially removes hydrogen and oxygen. Therefore, even if we are fortunate enough to recover organic material from the fossil record, its original chemical form is often substantially altered. Nevertheless, carbonization can preserve exquisite details of soft anatomy [SEE SECTION 10.2]. Leaves in coal and fine-grained sediments provide a good example.

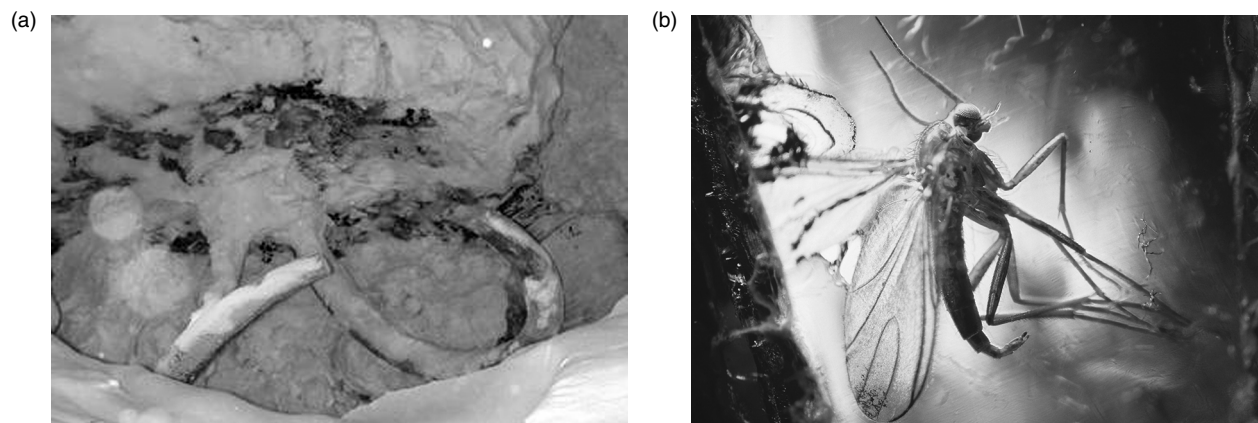
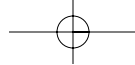


FIGURE 1.2 Common modes of fossilization. (a) Freezing: Woolly mammoth extracted from Siberian permafrost in 1999. (b) Preservation in amber: Eocene insect (midge) from the Baltic region of Europe (magnification $\times 9$). (c) Carbonization: Triassic **FERN** from the Carnic Alps of Germany. (d) Permineralization and petrification: Triassic petrified log from the Painted Desert of Arizona. (e) Replacement: Pyritized Ordovician trilobite (*Triarthrus eatoni*) from New York. (f) Recrystallization: Paleozoic **BRYOZOAN** from Tennessee. (g) Internal mold: **GASTROPOD** steinkern. (h) Cast: Upper Carboniferous **LYCOPSID** rooting structure (*Stigmaria*) from West Virginia. (a: Discovery Channel/Handout/X00561/Reuters/Corbis; b: Alfred Pasiaka/Photo Researchers, Inc.; c: John Cancalosi/Peter Arnold, Inc.; d: Eric and David Hosking/Corbis; e: Thomas Whitely; f: Unrug et al., 2000; g: R. A. Paselk, HSU Natural History Museum; h: West Virginia Geological and Economic Survey)

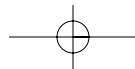
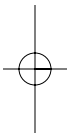
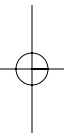
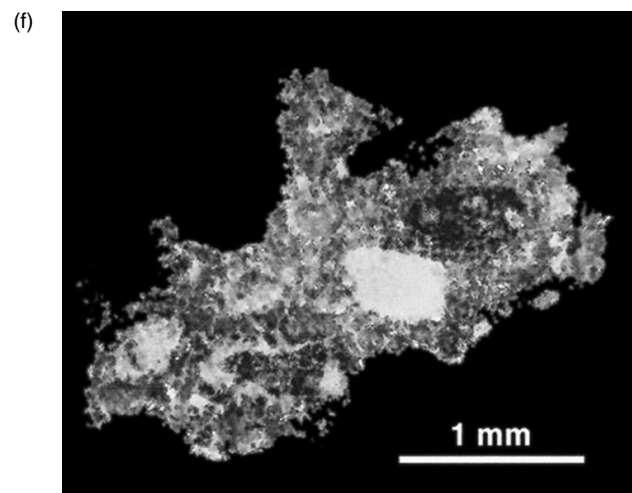
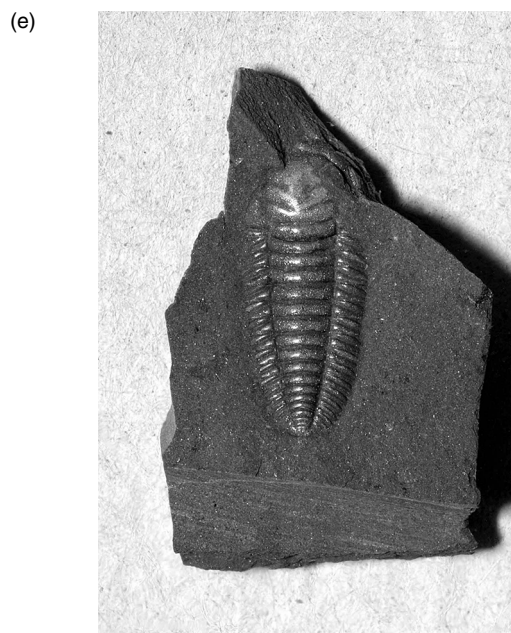
4. *Permineralization* (Figure 1.2d). As suggested earlier, the buried hard parts of organisms are not impervious to alteration. **Pore water** that percolates through a fossil-bearing unit can dissolve skeletal material, in some cases many years after it was buried by sediment in the first place. However, the pore water may be laden with dissolved materials that precipitate from solution in the spaces within the skeletal material. Through this process, substances such as silica, phosphate, and pyrite permeate the skeletal material, thereby hardening it, while preserving such fine structural details as growth bands, skeletal pores, and shell layers. A closely related process is **petrification**, which is the conversion of organic material to mineral material. Permineralization and petrification are both important in the preservation of plant tissue.
5. *Replacement* (Figure 1.2e). This process is similar to permineralization, except that the original skeletal material is itself replaced by the permeating materials, sometimes molecule-for-molecule, again preserving fine-scale structure. The exact nature of replacement depends on the details of pore-water chemistry. Examples include replacement by pyrite, FeS_2 (pyritization), silica (silicification), and phosphate minerals (phosphatization).
6. *Recrystallization* (Figure 1.2f). This is a very common process in which skeletal material that is subjected to

elevated temperature and pressure converts spontaneously to a thermodynamically more stable form (e.g., aragonite to calcite and amorphous silica to quartz). At a macroscopic scale, a recrystallized skeletal element may be difficult to distinguish from the original, but fine-scale structures may be virtually eliminated, as the element takes on the crystal structure of the new mineral.

7. *Molds* (Figure 1.2g) and *Casts* (Figure 1.2h). **Molds** are negative impressions of hard parts. Even when all of the original skeletal material has been dissolved away by pore water, an excellent replica of the hard part may still be preserved as a mold in the sediment that encases it, provided that the sediment is sufficiently fine grained. Some paleontologists have injected epoxy resin into carbonate rocks that contain molds and have then dissolved away the rock with acid to yield positive casts of the hard part. **Casts** also occur in nature when the original material first dissolves away, leaving a void that is filled subsequently with a secondary mineral substance or sediment. Of course, only surface features are preserved in molds and casts, but the level of detail preserved can be quite striking. Where sediment has filled in the empty skeleton of an organism, an internal mold or **steinkern** results. Here the internal features, such as scars showing muscle attachment, may even be preserved.



1.2 • FOSSIL PRESERVATION



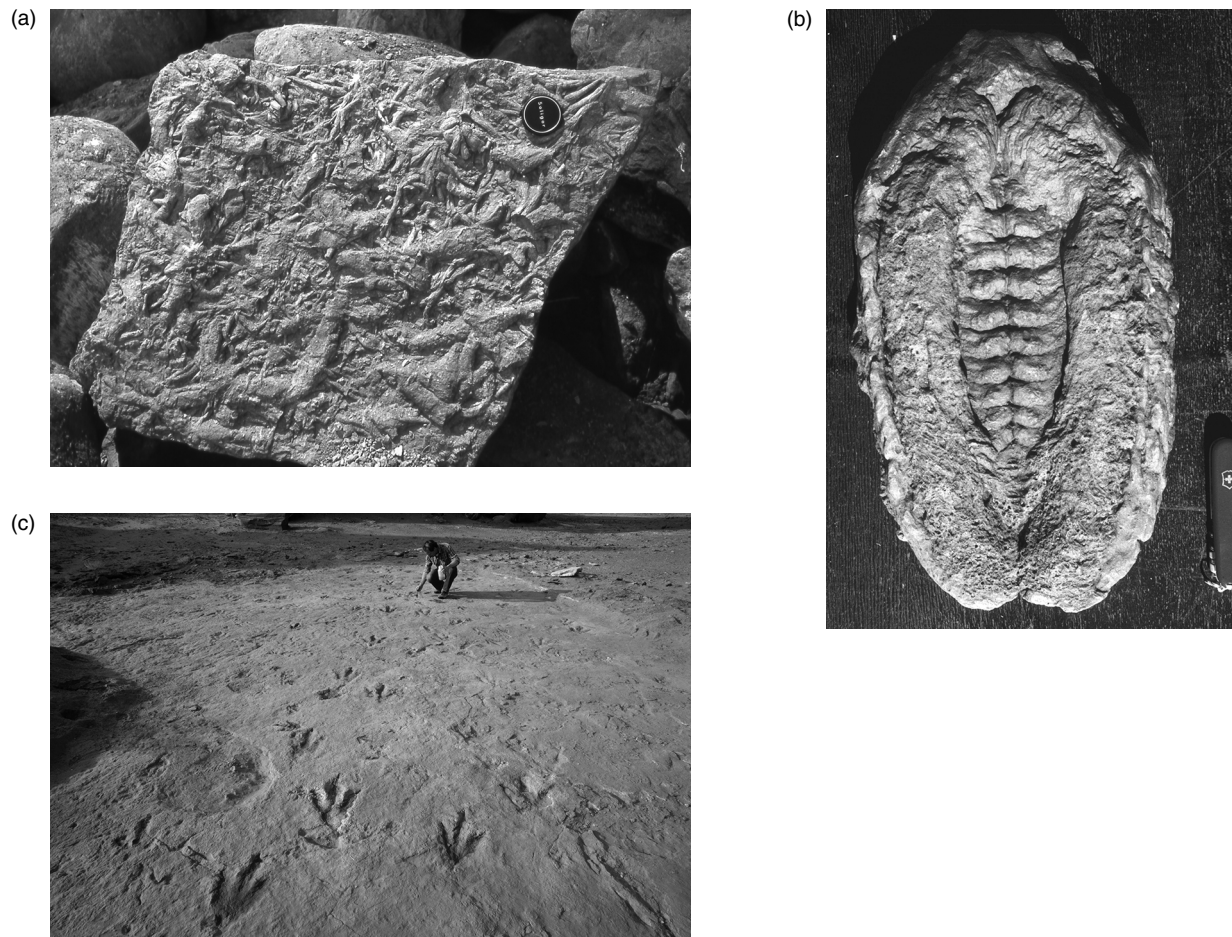


FIGURE 1.3 Examples of trace fossils. (a) Probable worm burrows from the Jurassic of England. (b) Resting trace (*Rusophycus*) of a trilobite from the Ordovician of Australia. (c) Dinosaur footprints from the Painted Desert of Arizona (a: Mike Horne, FGS, Hull, UK; b: From the collection of the Australian Geological Survey Organization, Canberra; c: Tom Bean/Corbis)

8. *Trace fossils* (Figure 1.3a, b, c). The modes of fossilization discussed up to now refer to **body fossils**, the remains of actual parts of organisms. Some organisms that are not preserved directly nevertheless leave behind traces of their activity. The most common examples of **trace fossils** include burrows and footprints. In most instances, it is difficult to know for certain the organism that made the trace, but the producers of some trace fossils can be identified. For example, Figure 1.3b illustrates a trilobite resting trace. Trace fossils may provide information concerning the behavior of organisms that is not available from body fossils alone. For example, large numbers of parallel trackways have suggested that certain dinosaur species traveled in herds. Evidence of activity by organisms can also be found directly on body fossils. Such traces include bite marks and boreholes.

Pseudofossils and Artifacts

The geologic record presents us with many inorganic structures resembling biological remains, such as mineral growths that branch like ferns, sediment degassing and dewatering features that look like animal trails and jellyfish, and sedimentary rip-up clasts that can be mistaken for arthropod fragments (Figure 1.4). It is essential to distinguish such **pseudofossils** from true remains of organisms. Morphological complexity, symmetry, and close resemblance to undoubtedly biologic remains are generally reliable, if not foolproof, criteria for recognizing true fossils.

The problem of pseudofossils has been especially prominent in the search for microbial life in the geologic record of the Archean and Proterozoic Eons. This is because inorganic, microscopic structures may falsely resemble microbes [SEE SECTION 10.7]. Paleontologists who

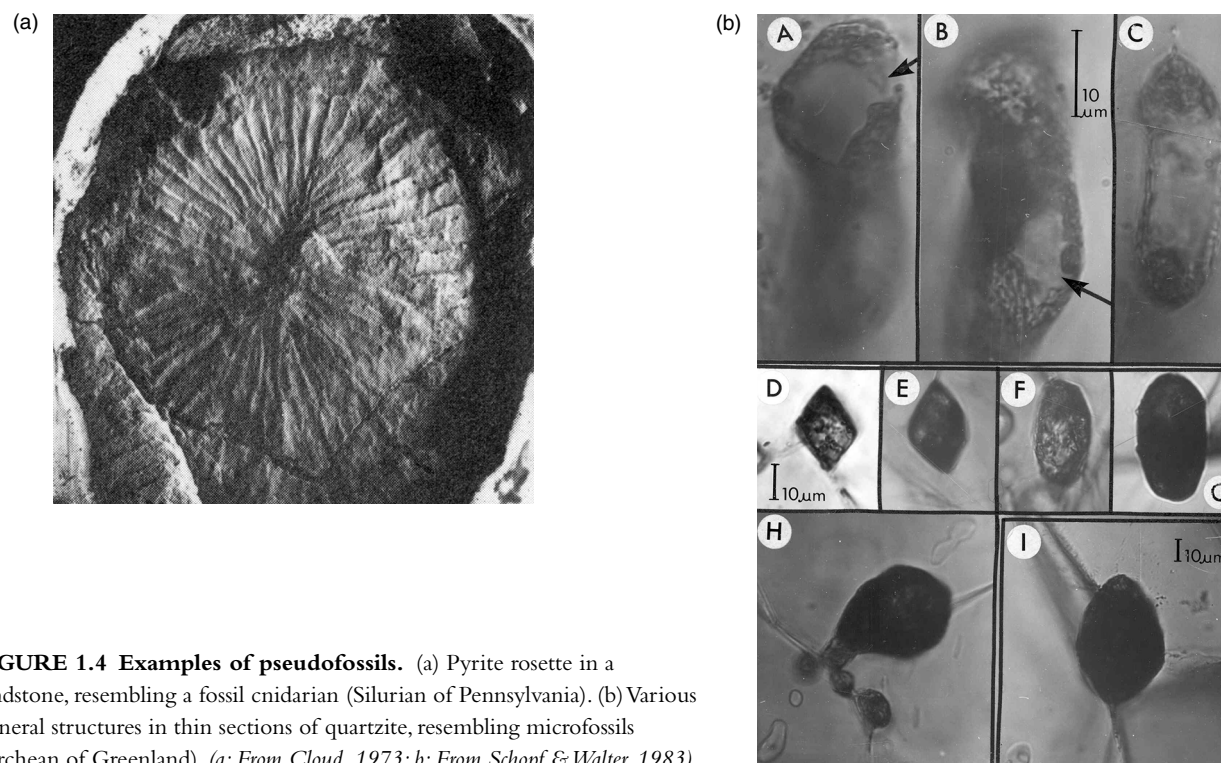


FIGURE 1.4 Examples of pseudofossils. (a) Pyrite rosette in a sandstone, resembling a fossil cnidarian (Silurian of Pennsylvania). (b) Various mineral structures in thin sections of quartzite, resembling microfossils (Archean of Greenland). (a: From Cloud, 1973; b: From Schopf & Walter, 1983)

study microbial life therefore look for a narrow size range within single species, for cells preserved in the act of dividing, and for other aspects of cellular structure (Figure 1.5). Although all organisms are subject to post-mortem degradation, particular problems arise with microbes. Experiments with living forms have shown that false “cells” and features can result as artifacts of preservation. Of particular interest is the fact that the preservation of **PROKARYOTES** (organisms composed of small, simple cells lacking a nucleus and other organelles) can produce artifacts that resemble the organelles of the cells in more complex **EUKARYOTES**.

Taphonomy

An understanding of fossilization processes is a great aid to paleontologists in interpreting the biological meaning of collected materials. Put another way: We know that a fossil assemblage will inevitably yield data that differ in

quantity and quality from those that would have been available from the living assemblage from which it was drawn. But if we understand these differences, we can adjust our interpretations of the record accordingly. These considerations fall within the field of taphonomy. Two broad aspects of fossilization are included under this umbrella: **biostratinomy**, in which the focus is on processes that affect a dead organism prior to burial; and fossil **diagenesis**, the processes that affect it after burial. Of course, an organism may be buried and exhumed several times after its death, so it may be subject to several phases of biostratinomic and diagenetic processes.

Experimental Approaches The direct study of fossilization processes is a central part of the field of **actuopaleontology**, a term derived from a German word meaning *paleontology of the present day*. To better understand the route to preservation, paleontologists have monitored the death, disintegration, and burial of

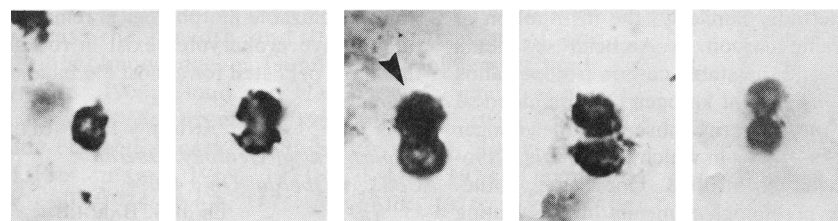
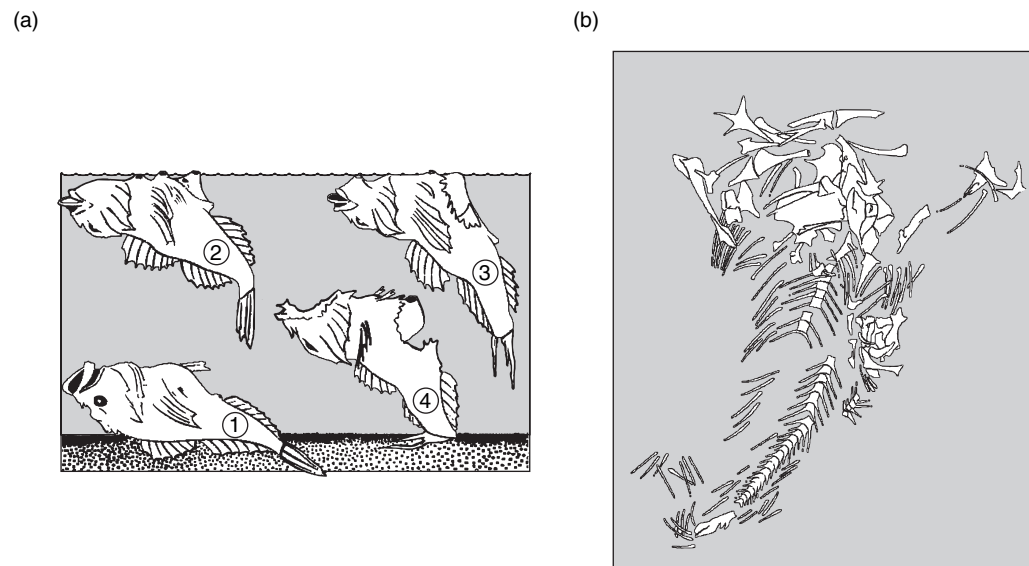


FIGURE 1.5 Photomicrographs of fossil cells in various stages of cell division. Material is from the Archean of South Africa. Magnification $\times 1600$. (From Knoll & Baghoorn, 1977)

FIGURE 1.6 An example of death and disintegration.

(a) Early stages (first four days) of decay in a carcass of the sea scorpion *Myoxocephalus scorpius*. An inflated stomach and gas bubbles from decomposition initially cause the carcass to float. Subsequently, gas escapes through tears that develop, and the carcass sinks. (b) Skeletal remains of *M. scorpius* on the sea floor after three months of exposure in agitated waters. (From Schäfer, 1972)



many kinds of organisms in the field (Figure 1.6). In the laboratory, they have simulated processes of destruction in ways that permit the control of experimental conditions. A common laboratory approach is to place skeletal material in tumblers with abrasives, such as pebbles, and to turn the tumblers to simulate transport and other agents of mechanical destruction.

For example, Susan Kidwell and Tomasz Baumiller (1990) ran a series of tumbling experiments on two species of the **ECHINOID** genus *Strongylocentrotus* after first allowing carcasses to decay for varying lengths of time in

a number of temperature and oxygenation conditions. They found that variations in the degree of oxygenation during decay had little effect on the tendencies of these echinoids to disintegrate during tumbling. However, variations in temperature dramatically affected tumbling results (Figure 1.7). The number of hours of tumbling required to cause near total disintegration of *S. purpuratus* carcasses was significantly greater among specimens allowed to decay in cold water (11°C) than it was among specimens allowed to decay in warmer water (23°C or 30°C). Colder conditions evidently retarded the rate of

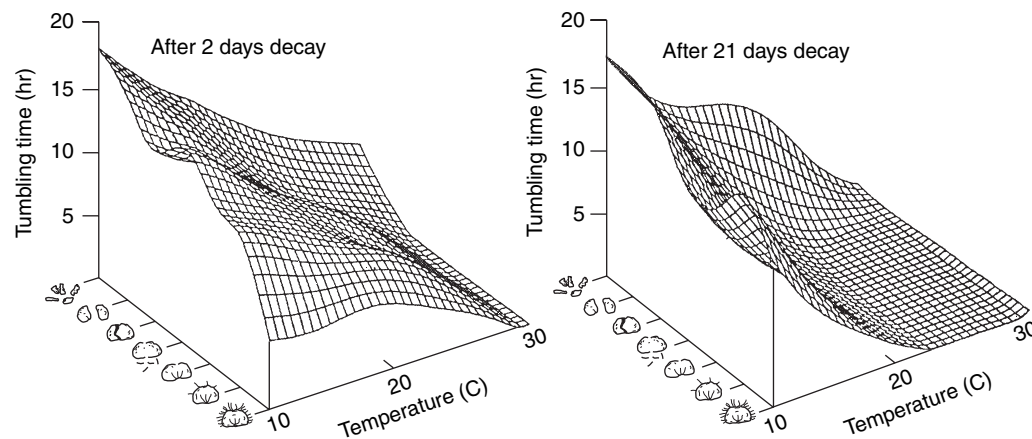


FIGURE 1.7 Experimental results from tumbling experiments on the echinoid *Strongylocentrotus purpuratus*. Surfaces show combinations of temperature, state of disintegration (indicated by the icons), and tumbling time for experiments in which echinoids were allowed to decay for 2 days and for 21 days prior to tumbling. Note that the pattern for the experiment involving 21 days of decay is not substantially different from that involving 2 days of decay. In both cases, the number of hours of tumbling required for major disintegration increases as the temperature decreases. (From Kidwell & Baumiller, 1990)

decay, thereby promoting the retention of soft tissues that help prevent disintegration. This was true whether the period of decay prior to tumbling was two days or 21 days, suggesting that the slowdown in the rate of decay at 11°C was so appreciable that a significant amount of soft tissue remained even after several weeks. These experimental results predict that there may be latitudinal and **bathymetric** trends in the preservation of echinoids, with better preservation, for the most part, in higher latitudes at moderate depth, where the water is cool and burial by storms is most common.

In another tumbling experiment, Benjamin Greenstein (1991) compared the durability of four echinoid genera. For each tumbled specimen, Greenstein calculated a *coefficient of breakage* (*CB*) based on assessment of the fragments greater than 2 millimeters (mm) in size that remained. The 2-mm cutoff was used as a practical limit below which fragments would probably not be recognized in the fossil record. The coefficient is calculated as:

$$CB = \frac{\text{Number of fragments} > 2 \text{ mm}}{\text{Weight of fragments} > 2 \text{ mm}} \times \frac{1}{\text{Weight percent of fragments} > 2 \text{ mm}}$$

Because a highly fragmented skeleton consists of a large number of pieces that collectively account for relatively little weight, such a skeleton will have comparatively high values for both the first term and the second term. Greater values of the *CB* therefore imply a greater degree of breakage of the skeleton. The second term helps to compensate for cases in which the skeleton is comparatively small to

begin with or becomes highly pulverized. A pulverized skeleton, with perhaps only a single remaining fragment larger than 2 mm, would yield a low *CB* if only the first term were used. However, because the weight percent of this one remaining fragment would likely be very small, the inclusion of this second term increases the *CB*.

Greenstein's experimental results are depicted in Figure 1.8. The four genera exhibited strikingly different degrees of breakage, with *Diadema* showing the most significant disintegration and *Echinometra* remaining intact. In light of his experimental results, Greenstein then considered the fossil records of the four families to which these genera belong. Paradoxically, a much greater percentage of species belonging to the family Diademataceae are preserved with tests intact than might be expected based on the tendency of *Diadema* to disintegrate rapidly. Greenstein showed, however, that fossil preservation in this family was strikingly bimodal: In most cases, specimens are preserved either in a highly fragmented state or nearly intact, with intermediate states of preservation barely represented. This is testimony to the fragility of the diadematacean skeleton. A diadematacean must be buried rapidly to avoid rapid disintegration; in cases when it is buried rapidly, it is preserved in a relatively complete state.

Taphonomic experiments have also assessed the chemical transitions associated with the decay and preservation of soft tissue [SEE SECTION 10.2]. For example, Stephen Grimes et al. (2001) subjected twigs of the plane tree to a variety of chemical environments meant to promote the precipitation of pyrite in association with decaying plant matter. Most experiments failed

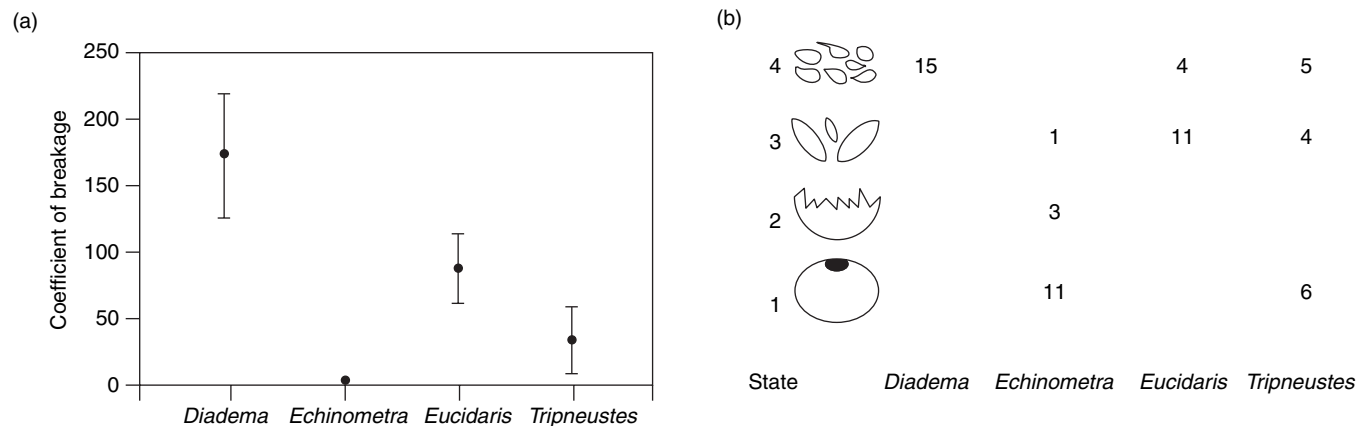


FIGURE 1.8 Experimental results from echinoid tumbling experiments. (a) Mean coefficient of breakage of four different echinoid taxa, each represented by 15 tests. Error bars show two standard errors of the mean (see Box 3.1). Schematic illustrations of the extent of breakage exhibited by the tumbled tests and the corresponding number of tests. (From Greenstein, 1991)

to yield pyrite. Rather, very particular combinations of sulfur, iron, oxygen, and organic concentrations were required in the lab. Presumably the requirements in nature would also be very specific. Significantly, one of the experiments that yielded no pyrite was one in which bacteria were not introduced. This is one of many studies to show that the chemical changes brought on by

microbial decay—including depletion of oxygen—facilitate mineral precipitation within and on soft tissues.

Assessment of Recent Subfossil Assemblages Paleontologists have also directly evaluated the extent to which **subfossil** assemblages that are accumulating today faithfully represent the living assemblages from which they

Box 1.1

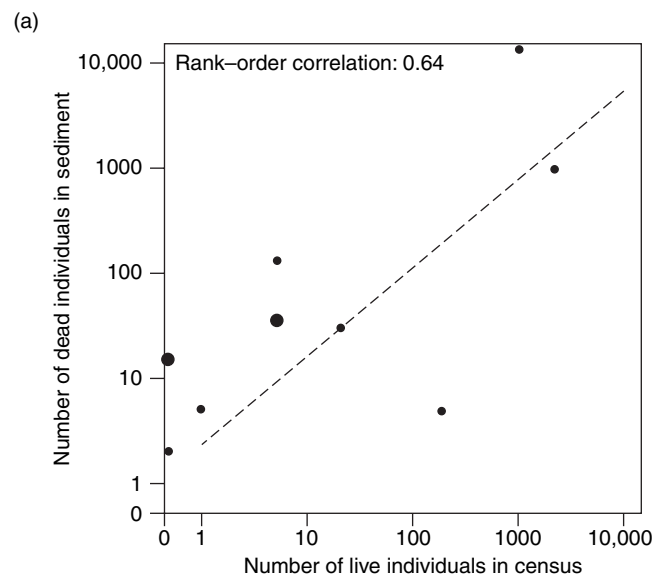
LIVE-DEAD COMPARISONS

In a broad survey of previous studies of living communities and their subfossil counterparts, Kidwell (2001) assessed whether the same roster of species tended to be present in life and death assemblages drawn from the same location, and whether they exhibited similar abundances. Figure 1.9a depicts one of these comparisons, from a tidal creek in California. Eleven species were found; their abundances in the live sample are plotted on the x axis, and their abundances in the sample of dead shells within the sediment are plotted on the y axis. Three of the species, plotted as zeroes on the x axis, were found as dead shells but were not present in the live sample. It is clear from this plot that the more abundant a species is in the live sample, the more abundant it tends to be in the dead sample; that is, the live and dead abundances are positively correlated. It is also evident that the dead abundances are generally higher than the live abundances.

Various correlation coefficients [SEE SECTION 3.2] are used to measure the strength of association between two variables. In this case, the correlation between live and dead abundances was measured with a rank-order coefficient that considers only the relative order of the variable; abundances of 0, 5, 6, and 100, for example, would be represented by the ranks 4, 3, 2, and 1. Correlations [and many other statistics; SEE SECTION 3.2] are commonly expressed by their corresponding p -values. The p -value estimates the probability that a correlation could be as high as observed, due to sampling error, if there were in fact no association between the two variables. The lower the p -value, the more reliable the inference that there is a true correlation in the data. It is conventional to regard p -values of .05 or less as statistically significant, in other words, indicating a true correlation.

The comparison of Figure 1.9a has 3500 live individuals and yields a correlation of +0.64 (on a scale of -1 to $+1$), with a p -value of about .04. This comparison is shown in Figure 1.9b, where the number of live individuals is on the x axis and the p -value on the y axis. This figure also includes 42 other comparisons from other localities. The horizontal dashed line marks the p -value of .05; results below this are considered statistically significant. Many of the comparisons do not yield significant correlations between live and dead abundances.

In the comparisons of Figure 1.9b, however, shells were collected with nets and sieves that have a mesh size of 1 mm or less; thus, shells at the smaller end of the size spectrum were included in these samples. Smaller shells are more susceptible to post-mortem destruction and transport. Moreover, live samples that include small shells are more likely to be sensitive to whether or not there has been a



were drawn. Collectively, these so-called live–dead investigations have sought to establish the degree of spatial and temporal resolution likely to be preserved in fossil assemblages. Live–dead comparisons thus provide one of the principal ways to assess the quality of the fossil record.

In cases where data are available to compare the species composition of skeletal remains with live sam-

ples drawn from the same settings, the relative abundances of species in living communities (**life assemblages**) tend to be maintained rather well in associated subfossil accumulations (**death assemblages**). This was demonstrated by Susan Kidwell (2001) in a comprehensive comparison of live and dead mollusc shells in a variety of marine settings (Box 1.1).

recent influx of larvae into the population. Figure 1.9c thus depicts a second set of comparisons, those that excluded the smallest shells by sampling with mesh sizes greater than 1 mm. These comparisons on the whole yield lower p -values and fewer

p -values above .05. In other words, there is a closer correspondence between live and dead abundances. Most of the comparisons that fail to yield significant correlations involve small data sets, with live abundances less than 100.

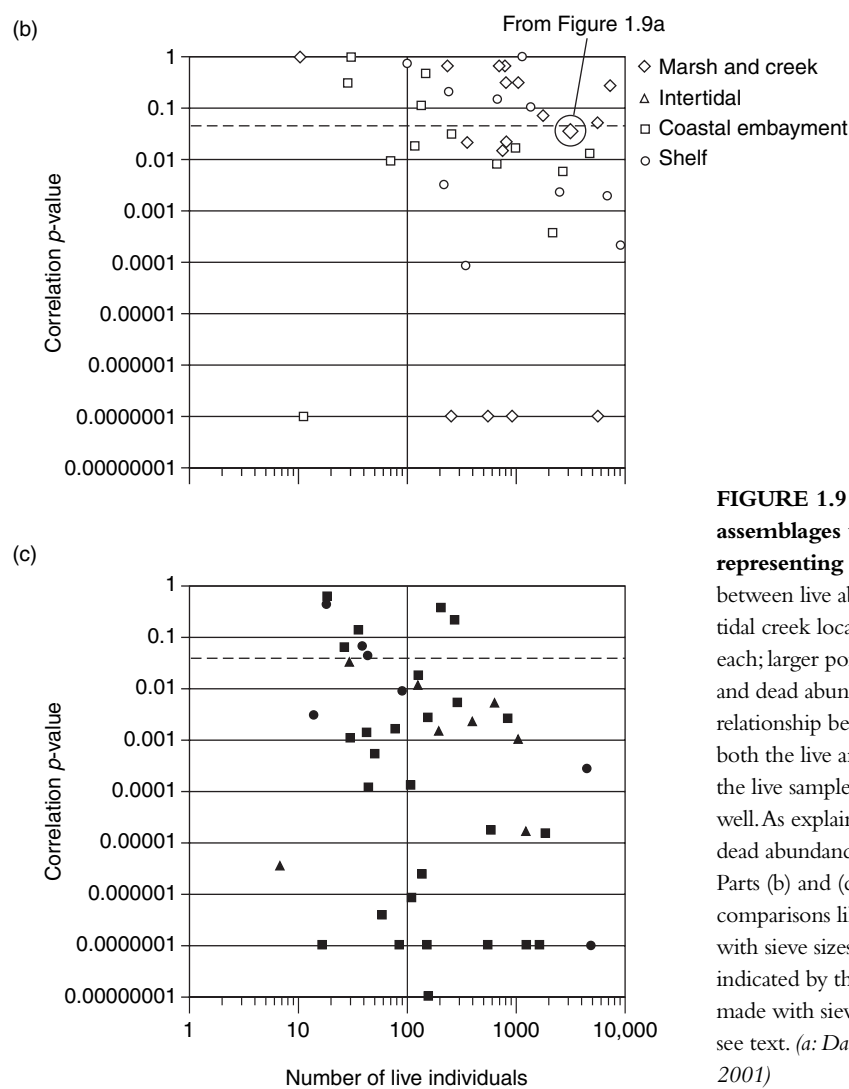


FIGURE 1.9 Kidwell's (2001) comparison of life assemblages versus death assemblages for 85 collections representing a variety of marine settings. (a) Comparison between live abundances and dead abundances of 11 species at a tidal creek locality in California. Small points represent one species each; larger points each represent two species with the same live and dead abundances. The dashed line shows the trend in the relationship between live and dead abundances for species found in both the live and dead samples. Species that are more abundant in the live sample tend to be more abundant in the dead sample as well. As explained in the text, the correlation between live and dead abundances is statistically significant with a p -value of .04. Parts (b) and (c) illustrate live abundances and p -values for 85 comparisons like that of part (a). (b) Forty-three collections made with sieve sizes of 1 mm or less. The comparison in part (a) is indicated by the large circled diamond. (c) Forty-two collections made with sieve sizes greater than 1 mm. For additional discussion, see text. (a: Data from MacDonald, 1969; b and c: Data from Kidwell, 2001)

Earlier we cited time averaging as one reason that a death assemblage often contains more species than the corresponding life assemblage. The analysis of Box 1.1 is fairly typical in illustrating a related reason: The death assemblage often contains more individual specimens than the life assemblage and is therefore more likely to capture the rarer species.

Comparisons between life assemblages and subfossil accumulations also indicate that death assemblages tend to retain excellent environmental fidelity, reflecting variation in species composition even at spatial scales as fine as tens of meters. However, the fidelity of death assemblages holds only for the readily preservable elements of the assemblage, and sometimes more strictly only for a single biologic group such as molluscs. It is unlikely that a fossil assemblage will provide a faithful rendition of the entire living assemblage from which it is derived. As discussed earlier, the loss of soft-bodied organisms, as well as organisms with fragile skeletons, is usually inevitable.

Assessment of Ancient Assemblages: Taphofacies The term **facies** in general refers to the characteristics of sedimentary rocks. **Taphofacies** are suites of fossils characterized by particular combinations of preservational features. In their pioneering discussions of taphofacies, Carlton Brett and Gordon Baird (1986) brought together factors such as post-mortem transport, degree of exposure, water oxygenation, sedimentary chemistry, skeletal robustness, and the number of articulated elements that compose the skeleton. The taphofacies approach provides an opportunity to assess the extent to which a life assemblage is altered during the formation of a fossil assemblage, but it also provides a diagnostic tool for paleoenvironmental analysis.

The application of the taphofacies concept is illustrated here for trilobites of the Middle Devonian Hamilton Group in New York. Stephen Speyer and Brett assessed several taphonomic attributes of sampled trilobite assemblages that included the trilobites *Phacops rana* (Figure 1.10a) and *Greenops boothi*. Characteristics that were evaluated included the proportion of skeletal parts oriented in a convex-up direction, the degree of skeletal articulation, the proportion of enrolled individuals, and the proportion of skeletal remains that were associated with molted skeletons. On this basis, a suite of trilobite taphofacies can be recognized, which are related to a depth gradient and the degree of **terrigenous** sedi-

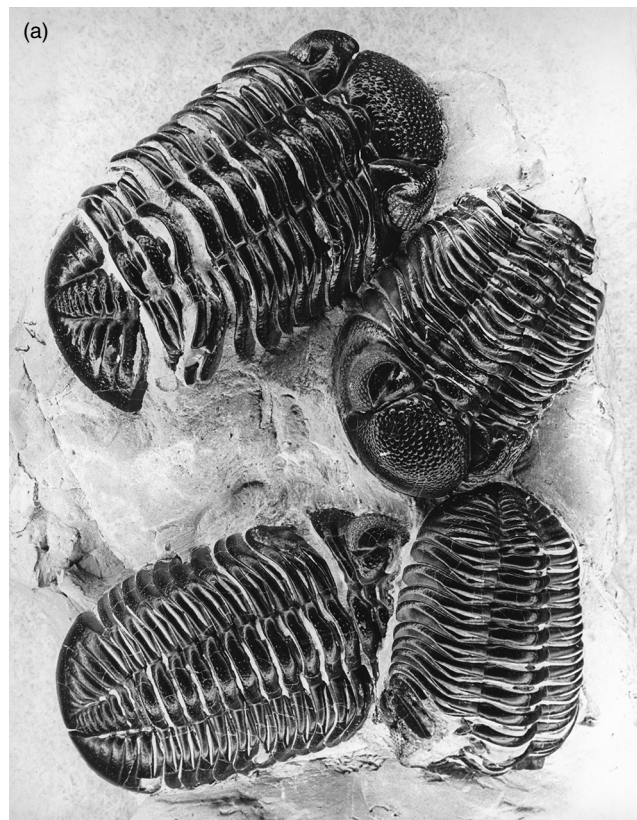


FIGURE 1.10 Speyer and Brett's (1986) assessment of trilobite taphofacies in the Middle Devonian Hamilton Group of New York. (a) Several well-preserved specimens of the trilobite *Phacops rana*. (Reprinted from Levi-Setti, 1975)

ment influx (Figure 1.10b). In general, shallower assemblages, which are characterized by coarser sediment, contained more highly fragmented material that tended to be oriented by current-related processes (e.g., taphofacies 1A in Figure 1.10b), except where sedimentation rates were comparatively high and skeletal material was buried rapidly or episodically. Articulation was more frequent in deeper water, with greater concentrations of skeletal material, including molts, in settings where there was not an overwhelming supply of terrigenous sediment (e.g., taphofacies 4A in Figure 1.10b).

Exceptional Preservation

Although the quality of preservation varies along a continuum, a handful of deposits have such exquisite preservation of organic and skeletal material that they are often discussed separately as fossil **Lagerstätten**, a

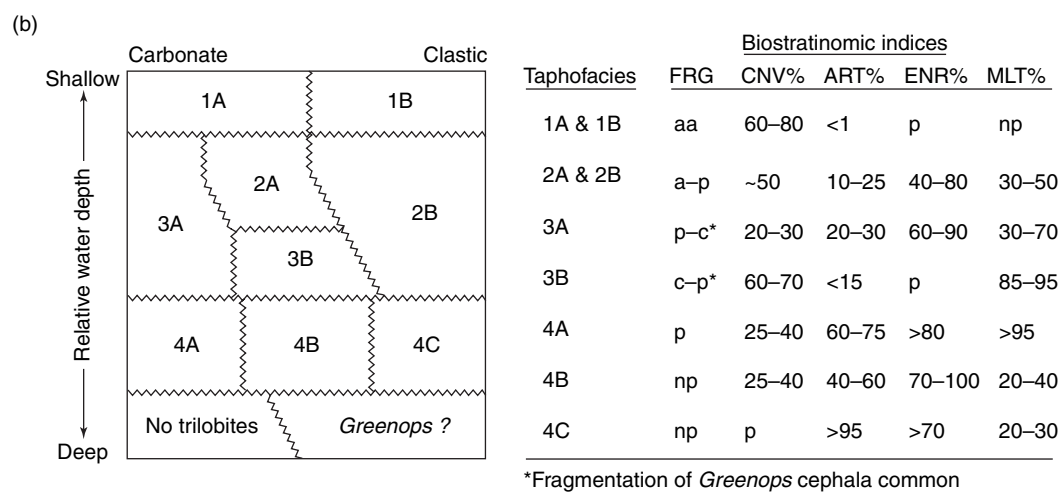
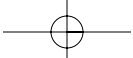


FIGURE 1.10 (cont.) (b) Delineation of a suite of Hamilton taphofacies based on biostratigraphic indicators, and their paleoenvironmental locations with respect to water depth and the nature of sedimentation. In general, specimens tend to be less fragmented and more complete (higher-numbered taphofacies) in deeper water. (Key: aa = very abundant; a = abundant; c = common; p = present but rare; np = not present. FRG = degree of fragmentation; CNV% = percent of specimens oriented convex-upright; ART% = percent of articulated individuals; ENR% = percent of specimens that were enrolled; MLT% = percent of articulated specimens that were preserved molts.) (From Speyer & Brett, 1986)

German mining term. These deposits have been very important in revealing aspects of biology that are ordinarily not preserved, such as the nature of arthropod limbs and other soft parts (Figures 1.11, 1.12), the chemical composition of vascular and other tissues in land plants (Figure 1.13), the feathers of early **BIRDS** (Figure 1.14),

and, in extremely rare cases, embryos (Figure 1.15). They have also opened windows onto whole communities during critical periods of time, such as the Middle Cambrian, an early phase in animal diversification that has been revealed by the Burgess Shale of British Columbia and other deposits elsewhere [SEE SECTION 10.2].

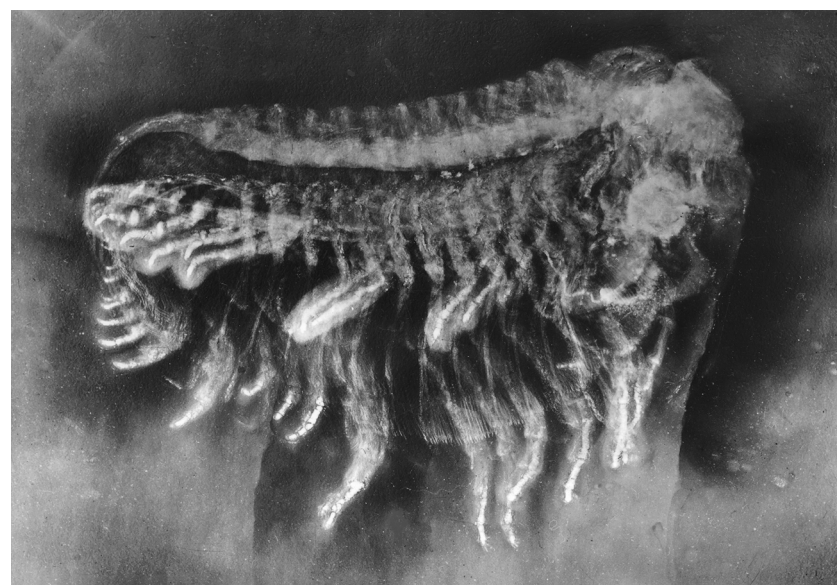
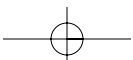


FIGURE 1.11 Radiograph of a trilobite from the Hunsrück Slate (Devonian of Germany). The specimen is unusual in showing an almost complete array of appendages. (X-ray taken by W. Stürmer, Erlangen, Germany)



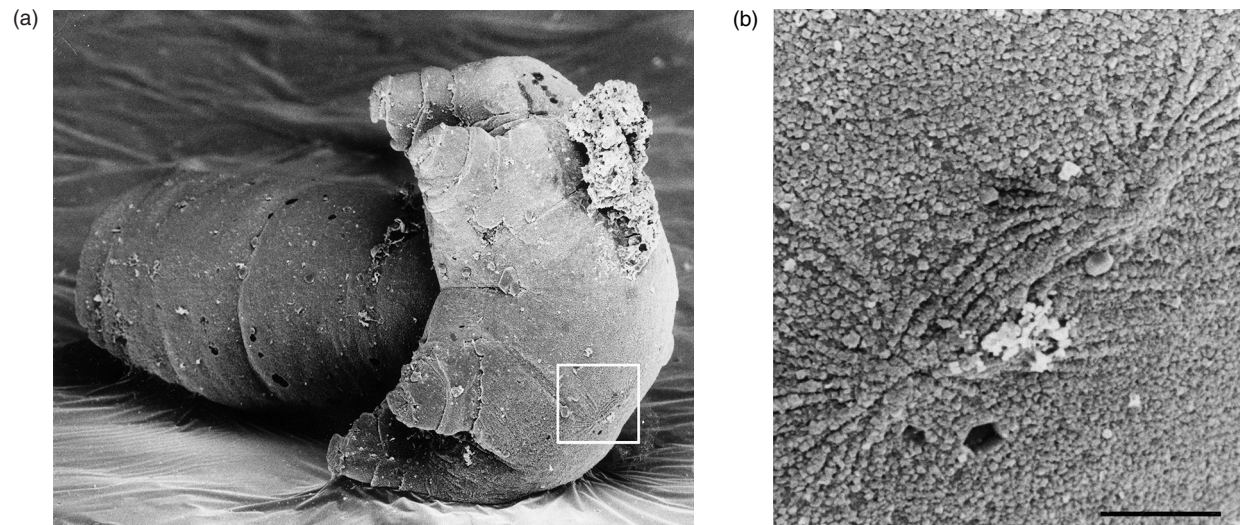


FIGURE 1.12 Specimen of the pentastomid *Heymsicambria kinnekullensis*, from the Upper Cambrian of Sweden. The material is phosphatized and shows exceptionally fine morphological details. (a) Anterior view of head. (b) Magnification of boxed area on Figure 1.12a, showing detail of papillae (sensory organs). Scale bar is 10 μm . (From Walossek & Müller, 1994)

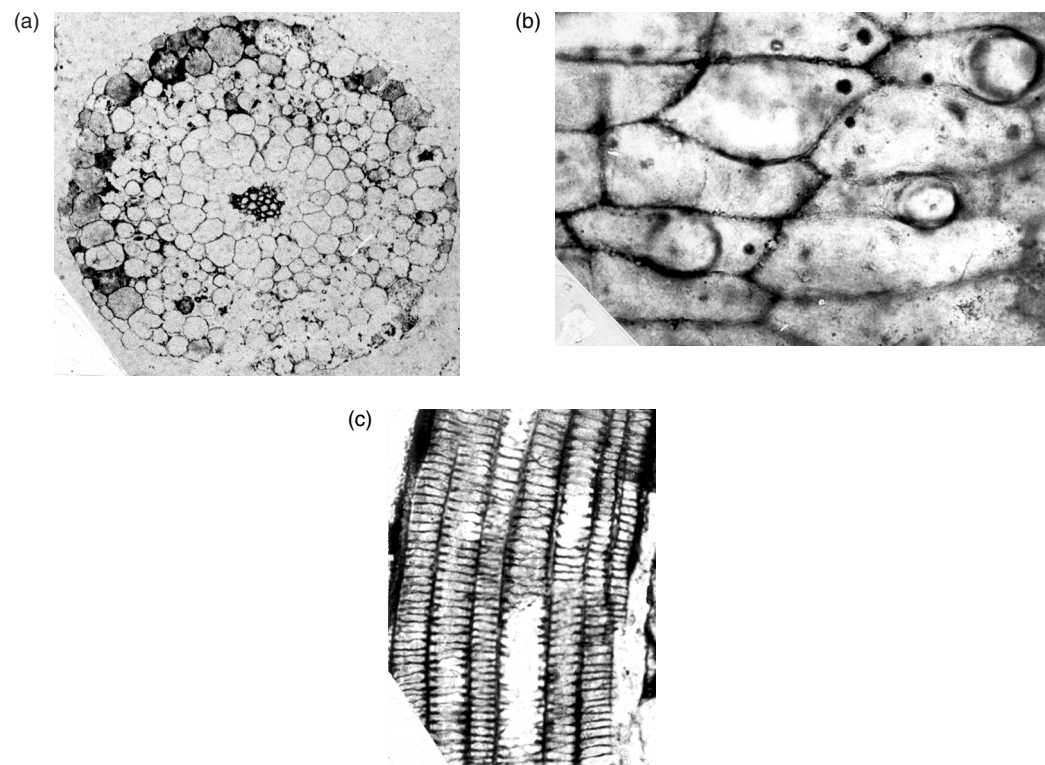


FIGURE 1.13 Specimens of the vascular plant *Trichopherophyton* from the Rhynie Chert (Lower Devonian of Scotland). (a) Cross section showing individual cells (magnification $\times 41$). The innermost dark cells are the conductive tissue xylem. The conductive phloem consists of the cells immediately surrounding the xylem. Most of the remainder of the specimen consists of cortex cells. (b) Magnification ($\times 187$) of cells. (c) A longitudinal section of xylem (magnification $\times 216$). Preservation in the Rhynie Chert is by petrification and permineralization. Original carbon is preserved, and this has been chemically analyzed to understand the evolution of vascular tissue by determining which tissues contained lignin (Boyce et al., 2003). (From Lyon & Edwards, 1991)

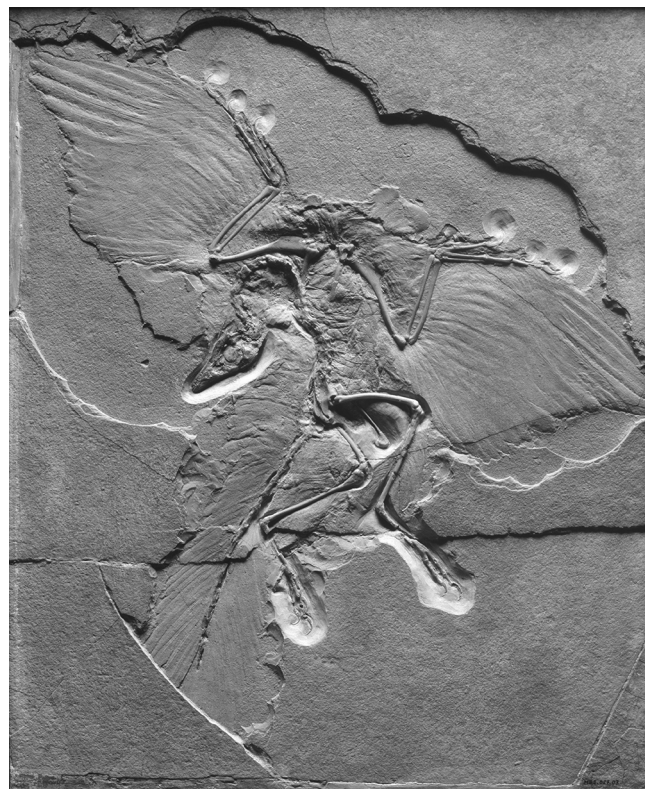


FIGURE 1.14 *Archaeopteryx*, the oldest known bird, from the Solnhofen Limestone (Jurassic of Bavaria). This fossil shows impressions of feathers. (Louie Psihoyos/Corbis)

1.3 SAMPLING OF THE FOSSIL RECORD

Rather than asking whether the record of a group of organisms is complete—for it never is—it is useful to consider whether the record is *adequate* for a particular purpose (Paul, 1982). Two issues must be addressed for any sample, each of which makes sense only in the context of specific paleontological questions. First, is the sample random (unbiased)? Second, are the quantities we measure sensitive to the size of the sample itself, even if it is unbiased?

Sampling inevitably involves error, but the science of statistics tells us how to deal with this. Suppose we collect a sample of 100 specimens from the Middle Cambrian Wheeler Formation in Utah and we find that 40 of them belong to the trilobite species *Elrathia kingi*. Provided that we do not preferentially collect the larger, more complete, or more attractive specimens—that is, provided that we sample randomly—our best guess is that the true proportion of *E. kingi* among the fossils in this formation is 40 percent. There would nevertheless be a well-defined margin of error associated with this estimate, and we would not be surprised if, upon collecting a second sample of 100 specimens, we found that as few as 35 or as many as 45 of them belonged to *E. kingi*. The larger the initial sample, the smaller the margin of error.

We can take pains to ensure that our sampling of the record is unbiased, but the record itself is strongly biased in favor of organisms that preserve more readily

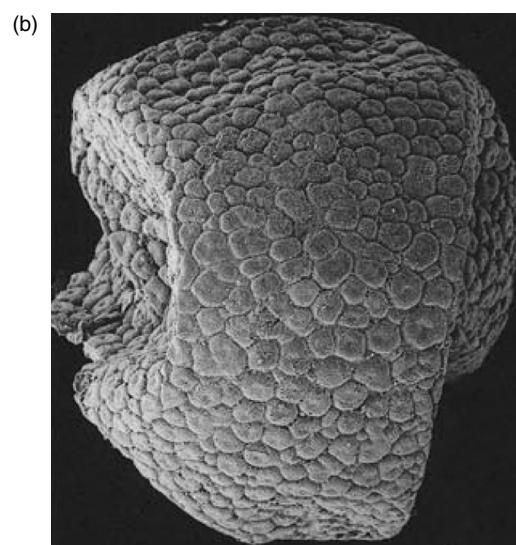


FIGURE 1.15 Phosphatized animal embryos from the Neoproterozoic of Guizhou, China. The width of the field of view is about 650 μm in part (a) and about 450 μm in part (b). (From Xiao & Knoll, 2000)

and that live where fossilization has occurred. Coming back to *E. kingi*, it would not be sound to conclude that 40 percent of all individuals that lived during the Middle Cambrian in the area of present-day Utah belonged to this species. Trilobites have mineralized exoskeletons, yet there would have been numerous soft-bodied species that left few if any fossil remains. The importance of such biases depends on the question we hope to address.

For estimating the relative proportions of individuals in an ancient community, differential preservation can represent a severe bias. (Another Middle Cambrian formation, the Burgess Shale, represents an unusual instance of soft-bodied preservation in the fossil record [SEE SECTION 10.2]. It has been estimated that, of well over 100 species known from this formation, less than 15 percent have hard parts that would be preserved under typical circumstances of fossilization.) For many questions, however, among-group variation in preservation potential is not so important. For example, if what interests us is evolutionary changes in body size within *E. kingi*, the preferential preservation of trilobites compared with that of other groups is irrelevant.

What about biases related to the size of the sample? Whether this matters depends on what we hope to measure from the sample. The average proportion of individuals in a sample that belong to a certain species generally does not depend on the number of individuals sampled. By contrast, the number of species recovered from a locality depends on the number of individuals sampled, as does the maximum body size recorded for a given species.

Ideally, the effects of sample size are reduced by standardizing the nature and extent of sampling as part of a study design—for example, collecting the same number of specimens from different formations if the goal is to compare the number of species among those formations. Often this is not feasible, as when we are analyzing data that have already been collected for other purposes; the standardization of the sample must therefore be performed statistically. A simple procedure for this after-the-fact standardization is **rarefaction** (Box 1.2), which estimates the number of species or other taxa that would have been found if a smaller number of individuals had been sampled.

All organisms, fossil and living, are classified not only into species but also into higher groupings or categories. [SEE SECTION 4.3]. At the higher end of the classificatory scale are taxonomic groups such as phylum and class. At the lower end of the scale are groups such as family and genus. We can also apply rarefaction to estimate how many

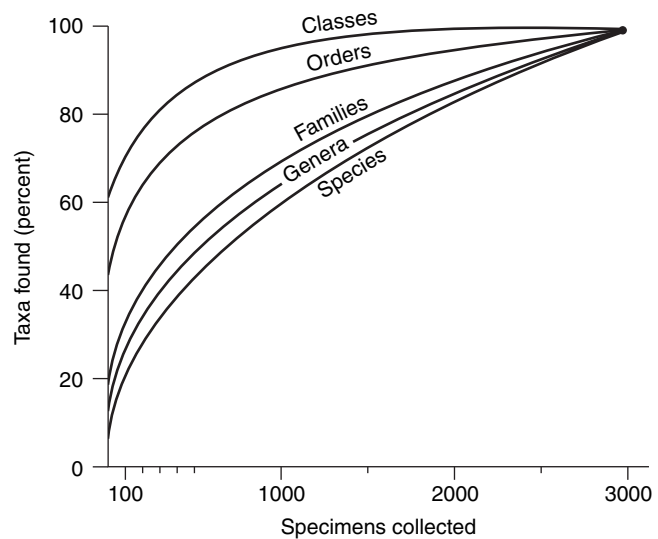


FIGURE 1.16 Rarefaction curves for molluscan fossils found in a well sample of Miocene age in Denmark (based on data from Sorgenfrei, 1958). The point at the upper right represents the actual sample. The curves estimate how many taxa would have been found had the sample been smaller.

genera, families, or other taxa would have been found if a smaller sample of individuals had been collected.

Figure 1.16 illustrates the rarefaction method with an example from the Miocene of Denmark. Table 1.2 shows the number of groups at each taxonomic level that were recovered from a sample of nearly 3000 individuals. Because the author of this study was interested only in molluscs, only one phylum was recorded. Three molluscan classes were present (**BIVALVIA**, **GASTROPODA**, and **SCAPHOPODA**). At the other end of the taxonomic scale, there were 86 species. As is almost always the case, each lower taxonomic level yielded a

TABLE 1.2
Numbers of Taxa Found in a Molluscan
Sample from Arnum Formation
(Miocene of Denmark)

2954 Specimens	
Phyla	1
Classes	3
Orders	12
Families	44
Genera	64
Species	86

SOURCE: Sorgenfrei (1958)

Box 1.2

RAREFACTION METHOD

To compute a rarefaction curve such as the species curve in Figure 1.16, it is necessary to know the number of individuals in the sample (N), the number of species (S), and the number of individuals found for each species (N_i , where $i = 1, 2, \dots, S$). There are several ways to compute the expected number of species that would be found in a smaller sample of n individuals, denoted $E(S_n)$. A simple approach is to program a computer to grab n individuals at random from the entire collection. For example, suppose there are $N = 25$ individuals distributed among three species with $N_1 = 15$, $N_2 = 8$, and $N_3 = 2$. The list of individuals is shuffled like a deck of cards, and the first n on the list are chosen. If we identify each individual with its species number, the initial list looks like this: 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 3 3. We randomly shuffle the list and end up with: 2 1 1 2 2 2 1 1 1 1 1 2 2 1 1 1 1 1 3 1 1 3 1 2 2. If we want to take a sample of $n = 10$ individuals, we simply read the first 10 off this list, and we end up with six individuals of species 1, four individuals of species 2, and zero individuals of species 3. Thus, two species were found in this sample of $n = 10$ individuals.

There is clearly random variation associated with this procedure. For example, another shuffling of the list yields: 3 2 2 1 2 1 1 1 2 2 1 1 3 1 1 1 2 1 1 1 2 2 1 1 1, with the result that all three species are found in the first 10 individuals on the list. For this reason, the randomization is carried out hundreds or thousands of times, and the results are averaged together. There is also an exact equation that produces the same results directly (see Raup, 1975).

In practice, the calculations are carried out for an arbitrary series of n values (all less than N) and each $E(S_n)$ thus produced yields one point on the rarefaction curve. Or if several samples are to be compared at a standard n , that n can be used for a single computation for each sample. It is also possible to compute the uncertainty attached to the estimated species numbers, that is, the variance of $E(S_n)$ (see Raup, 1975; see also Box 3.1).

In the case of the species rarefaction in Figure 1.16, N was equal to 2954 and S was 86. The most common species was represented by 818 individuals; 40 of the species had only one specimen each. A few of the computed values of $E(S_n)$ and its variance are given below:

Number of Specimens (n)	Expected Number of Species $E(S_n)$	Variance of $E(S_n)$
2500	79.66	5.42
2000	71.93	9.89
1500	63.14	12.59
1000	52.52	13.59
500	38.56	12.23
100	19.05	6.64
50	14.05	5.05
10	6.24	2.88

If rarefaction is to be done at higher taxonomic levels (as in Figure 1.16), data for genera, families, and higher categories are simply substituted for the species data and the same procedure is used.

larger number of taxa. If fewer than 2954 specimens had been collected, the number of taxa recovered would have been smaller, as shown by the rarefaction curves. This effect would have been more pronounced at the lower taxonomic levels. For example, the rarefaction equation predicts that, if 1000 individuals had been sampled, only about 60 percent of the 86 species would have been recovered, but over 80 percent of the orders would have been found.

This last result reflects an important and general aspect of sampling of the fossil record: *Sampling is more complete at higher taxonomic levels.* This is a necessary consequence of the nesting of taxonomic groups within one another. Each genus contains one or more species, each family contains one or more genera, and so on. Therefore, there will tend to be more individuals in any genus than in one of its component species, and more individuals in any family than in one of its component genera.

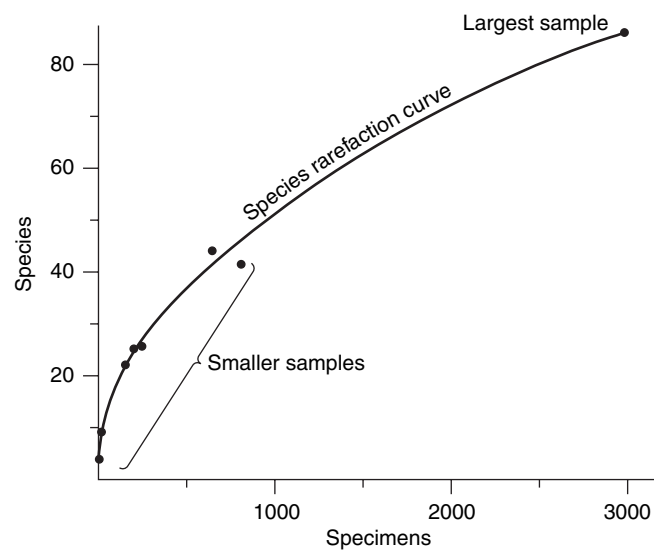


FIGURE 1.17 Effect of sample size on the number of species found in a fossil assemblage. The solid line is the species rarefaction curve from Figure 1.16, and the points represent other samples collected from above and below the main sample. (Based on data from *Sorgenfrei, 1958*)

In Figure 1.17, the effect of sample size on species number is shown in another way for the Danish data. The sample of 2954 individuals was the largest of eight samples taken from one formation. The other seven samples came from different stratigraphic intervals above and below the large sample. The numbers of specimens and species for each are plotted in Figure 1.17, along with the rarefaction curve for species in the largest sample, taken from Figure 1.16. The points for the small samples fall very close to the theoretical rarefaction curve, suggesting that the differences in numbers of species are just the result of sample size differences.

Figures 1.16 and 1.17 illustrate the general point that increased sampling tends to yield diminishing returns. Doubling the number of individuals sampled from a formation generally results in substantially less than a doubling of the total number of species recovered. The main reason for this is that a small number of species usually account for the vast majority of individuals. Therefore, repeated sampling tends to produce the more common species again and again; additional, rarer species are much less likely to be recovered.

It is important to keep in mind two points that are often misunderstood about rarefaction. First, it cannot be used for extrapolation—to estimate how many species would have been found had a larger sample been

taken. Second, although rarefaction curves often give the appearance of leveling off, the apparent flatness of a curve does not necessarily imply that the true quantity of interest, such as the number of species that actually lived at some time in the past, has nearly been reached. The most we can conclude from a nearly level rarefaction curve is that we may be unlikely to obtain much more information with modest amounts of additional sampling; enormous efforts could be required to find the rarest preserved species.

Measuring Completeness of the Fossil Record

When we discussed the observed diversity of brachiopods and bivalves earlier, we noted that knowing something of the relative completeness of different groups of organisms can help determine whether evolutionary differences among them are likely to be artifacts of differences in preservation potential. It is therefore important to have some means of estimating **paleontological completeness**. Completeness can be expressed as the probability of sampling a given taxon within a specified interval of time, or as the probability of sampling the taxon at least once within its entire duration.

The simplest way to measure the probability of sampling per time interval is to compare the number of time intervals in which a taxon is actually sampled with the number of intervals during which we know it existed and therefore had the opportunity to be sampled (Box 1.3). An interval of time during which a taxon existed but from which it is not sampled is a **gap** in the stratigraphic range of the taxon [SEE SECTION 6.4].

The tabulation of gaps in sampling requires a substantial amount of information, namely the presence or absence of each taxon in each interval of time. If these data are not available, there are a number of indirect ways to estimate sampling probability. One is based on the expectation that a lower sampling probability will lead to a greater proportion of taxa being sampled from only one interval of time, regardless of how long-lived they may in fact have been (Box 1.3). Table 1.3 presents some sampling estimates based on this approach. For skeletonized animals, sampling probabilities range from about 10 percent to over 90 percent per genus per 5-million-year time interval.

To estimate completeness summed over the durations of taxa, we can simply compare the number of living taxa within some group with the number that

TABLE 1.3

Estimated Completeness of Genera Within
Some Paleontologically Important Groups

Group	Probability of Preservation per Genus per Time Interval
Sponges	0.4–0.45
Corals	0.4–0.5
Polychaetes	0.05
Malacostracan crustaceans	0.2–0.35
Ostracodes	0.5
Trilobites	0.7–0.9
Bryozoans	0.7–0.75
Brachiopods	0.9
Crinoids	0.4
Asterozoans	0.25
Echinoids	0.55–0.65
Bivalves	0.45–0.5
Gastropods	0.4–0.55
Cephalopods	0.8–0.9
Graptolites	0.65–0.9
Conodonts	0.7–0.9
Cartilaginous fishes	0.1–0.15
Bony fishes	0.15–0.3

SOURCE: Foote & Sepkoski (1999)

NOTE: Time intervals are roughly 5 million years long on average. Estimates are based on the principle that the probability of preservation is likely to be lower in groups where a higher proportion of genera are confined to a single time interval (Box 1.3). Details of the calculation are found in Foote and Sepkoski (1999).

are known as fossils. Tables 1.4 and 1.5 present tabulations of this kind, which of course cannot be compiled for completely extinct groups. These tabulations show the expected effects of taxonomic level. A greater proportion of genera have a fossil record compared with the species of the same group, and likewise for families versus genera.

A second way to estimate the overall proportion of taxa sampled was suggested by paleontologist James Valentine (1970). This is to compare the total number of taxa known as fossils with an estimate of the number that have ever lived. For example, some 300,000 animal species have been described from the fossil record. How does this compare with the number of animal species that are likely to have lived over the Phanerozoic? This second number

TABLE 1.4

Proportion of Living Taxa with
a Fossil Record

Group	Taxonomic Level	Percent
Sponges	Family	48
Corals	Family	32
Polychaetes	Family	35
Malacostracan crustaceans	Family	19
Ostracodes	Family	82
	Genus	42
Bryozoans	Family	74
Brachiopods	Family	100
	Genus	77
Crinoids	Family	50
Asterozoans	Family	57
	Genus	5
Echinoids	Family	89
	Genus	41
Bivalves	Family	95
	Genus	76
Gastropods	Family	59
Cephalopods	Family	20
Cartilaginous fishes	Family	95
Bony fishes	Family	62
Arachnids	Genus	2
	Species	< 1

SOURCES: Raup (1979); Foote & Sepkoski (1999); Valentine et al. (2006). Data are global.

TABLE 1.5

Proportion of Living Molluscan Taxa in
the Californian Province with a Pleistocene
Fossil Record in this Region

Group	Taxonomic Level	Percent
Bivalves	Family	91
	Genus	84
	Species	80
Gastropods	Family	88
	Genus	82
	Species	76

SOURCE: Valentine (1989)

Box 1.3

SELECTED MEASURES OF PALEONTOLOGICAL COMPLETENESS

We first consider the probability of sampling a taxon per unit time interval (Paul, 1982). In the hypothetical data of Figure 1.18, gaps in sampling are seen as time intervals during which a species existed but left no known fossil record. The fewer such gaps, the higher the estimated probability of sampling. For example, species 1 persisted through four time intervals between its first appearance in interval 1 and its last appearance in interval 6. Thus, it had four opportunities to be sampled. Of these four intervening intervals, it is known only from interval 5; intervals 2, 3, and 4 mark gaps in the record of species 1. Its estimated sampling probability is therefore 1/4, or 25 percent per interval. Because there are few observa-

tions for each individual species, the margin of error of the estimated sampling probability tends to be quite high. By combining data for many species, a more reliable estimate of average sampling probability can be obtained. Gaps can also be tabulated for individual time intervals to determine how sampling probability varies over time.

Compilations of stratigraphic information often report only the times of first and last occurrence of fossil taxa, not the intervening occurrences shown in Figure 1.18. Such data can be used to estimate sampling probability with a method that relies on mathematical formalization of a simple, intuitive principle: Because incomplete sampling tends to shorten ob-

Time interval	6	x	x				x	x			
	5	x		x		x			x	x	x
	4		x			x	x	x	x		
	3		x		x		x				
	2		x	x	x	x					
	1	x									x
	Species	1	2	3	4	5	6	7	8	9	10
Opportunities for sampling (excluding range endpoints)	4	3	2	—	2	—	1	1	—	3	16
Occurrences (excluding range endpoints)	1	2	0	—	1	—	0	1	—	0	5

FIGURE 1.18 Schematic illustration of gap analysis used to estimate average sampling probability of a group of species. Each × marks a time interval in which the corresponding species is sampled; intervening blank spaces are gaps in the record of the species. The number of occurrences for each species is tabulated as the number of intervals in which the species is found, excluding the intervals of first and last appearance. This is compared with the number of opportunities for sampling—that is, the number of time intervals during which the species had a chance either to be sampled or not. This is simply the sum of time intervals between the first and last appearance. Because a species necessarily must be sampled in its intervals of first and last occurrence, these intervals are not included in the tabulations; to include them would overestimate the sampling probability. In this case, there are 16 opportunities for sampling and 5 occurrences; both numbers exclude first and last appearances. Thus, the estimated sampling probability of these species is 5/16, or 31 percent per time interval.

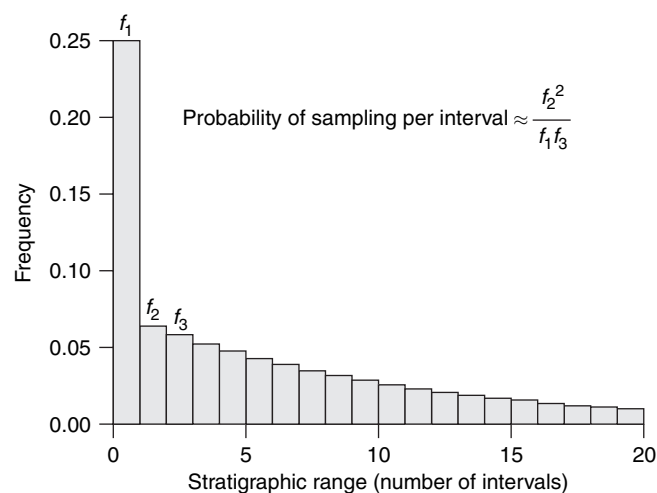


FIGURE 1.19 Frequency distribution of stratigraphic ranges of taxa, assuming incomplete but uniform sampling. Sampling probability per unit time interval can be estimated from the frequencies of taxa with ranges of one, two, and three intervals. (After Foote & Raup, 1996)

served stratigraphic ranges, the proportion of taxa that are known from only a single stratigraphic interval should be inversely proportional to the quality of sampling. Assuming that sampling probability is constant over time, the probability of sampling per unit time can be estimated as $(f_2)^2 \div (f_1 f_3)$, where f_1 , f_2 , and f_3 are the numbers or relative proportions of species with preserved stratigraphic ranges of one, two, and three intervals (Figure 1.19; Table 1.3). Further details can be found in Foote and Raup (1996).

To compare the number of known fossil species with the estimated number that actually existed, we restrict our consideration to the paleontologically important groups; strictly soft-bodied organisms are ignored. Estimating the total number of species over the course of the Phanerozoic Eon requires that we know the average longevity of species—which tells us how often existing species became extinct and were replaced by new species—as well as the level of diversity during the Phanerozoic. Using methods similar to those we will treat in detail in Chapter 7, we can estimate the typical longevity of marine invertebrate species as roughly 4 million years. In other words, about 25 percent of existing species became extinct every million years.

The number of living species that have been described is about 1.5 million, although there is great uncertainty in this number. If we focus on the paleontologically important groups, present-day diversity is about 150,000 species. The path from an initial diversity near zero to the current diversity of 150,000 is hard to know, because observed diversity severely underestimates the true number of species that were alive at any time in the past. We can, however, take an approach that almost surely overestimates past diversity, and therefore leads to a minimum estimate of the proportion of species sampled. Suppose we assume that the present-day level of diversity was attained immediately at the beginning of the Cambrian Period and has been maintained since then. Then 25 percent of 150,000 species, or 37,500 species, became extinct and were replaced by new species every million years. In rough terms, the Phanerozoic is 550 million years long. This leads to an estimate that there have been $150,000 + (37,500 \times 550)$, or about 21 million species. Comparing this with the 300,000 described fossil species implies that between 1 percent and 2 percent of species are known as fossils.

depends on how the number of species has varied over geologic time [SEE SECTION 8.3], and the rate at which species have become extinct and have been replaced by new species [SEE SECTION 7.2]. Carrying out the relevant calculations (Box 1.3) yields estimates that around 20 million species in the paleontologically important groups have existed over the past half billion years. In other words, somewhat over 1 percent of all animal species in the readily preserved groups are known from the fossil record. At first glance, this may seem like a small percentage, but in fact, reliable statistical inferences in many fields are routinely drawn with much smaller samples.

To take just one example, the typical national presidential poll in the United States uses a sample of about 1500 voters, out of a voting-age population of over 200 million. Thus, the sample represents less than 0.001 percent of the eligible voters, yet such polls tend to be fairly accurate as predictors of election results.

Completeness, of course, varies from group to group. Groups such as trilobites, brachiopods, molluscs, and some classes of **ECHINODERMS** are much better represented in the fossil record than the 1 percent figure would suggest.

How can we reconcile the estimate of 1 percent completeness with the tabulations like that of Table 1.5—showing that nearly 80 percent of the marine molluscan species living in California today are known from the Pleistocene fossil record? One reason for the discrepancy is, of course, that the bulk estimate of animal completeness covers not just molluscs, which are relatively well preserved, but also groups such as **STARFISH**, crustaceans, and sponges, which are not so well preserved. A more important reason reflects the distinction between **local completeness** and **global completeness**. Where there is some preserved fossil record, we often find that its completeness is rather high. Fossiliferous rocks have a patchy geographic distribution, however. For any given interval of geologic time, most localities have left no sediments that are exposed today.

The data on modern and Pleistocene molluscs from California illustrate the point that entering the fossil record is only part of the picture. The record itself must escape subsequent erosion and metamorphism, and must remain unobscured by younger, overlying sediments for the species that are initially fossilized to contribute to our knowledge of the history of life. The fact that local completeness is often high is important for the study of evolution, for it implies that evolutionary patterns within locally preserved species may often be represented with considerable fidelity in the fossil record.

1.4 TEMPORAL CHANGES IN THE NATURE OF THE FOSSIL RECORD

Because many of the geologic and evolutionary processes studied with fossil data act over long timescales (tens to hundreds of millions of years), it is important to understand how the nature of the fossil record has changed over such timescales and how this may influence our interpretation of paleontological data. We already touched on this issue in discussing the relationship between the number of fossil species and the exposed area of sedimentary rock (Figure 1.1).

Bioturbation

The intensity of marine bioturbation has evidently increased over the past 500 million years of animal life. Figure 1.20 shows one way that this has been documented. This figure illustrates the ichnofabric index, which provides a rough measure of bioturbation preserved in sedimentary rocks. (The Greek prefix *ichno-* refers to “trace.”) Analysis of a sequence of Cambrian and Ordovician sedimentary rocks shows an increase in the average ichnofabric index, portrayed in Figure 1.21. This corresponds to the evolution and diversification of animal groups that exploited the sediment as habitat and as a food source.

The first step marks the appearance of trilobites within the Lower Cambrian. The reasons for the second step, between the Middle and Upper Ordovician, are not so clear. It does not coincide with the appearance of a major new group of hard-bodied animals, although it does come shortly after a pronounced diversification of marine taxa that would come to dominate Paleozoic marine settings [SEE SECTION 8.4]. It is therefore possible that this step marks a behavioral innovation in some skeletal group or the evolution of a new group of soft-bodied animals. Whatever their causes, it is likely that these increases in bioturbation resulted in an increase in time averaging. They may also have led to greater physical disturbance and disaggregation of carcasses and to a reduced probability of soft-part preservation.

Skeletal Mineralogy

The relative abundance of various shell-forming minerals has changed over the history of life. One major change that is potentially important for the quality of

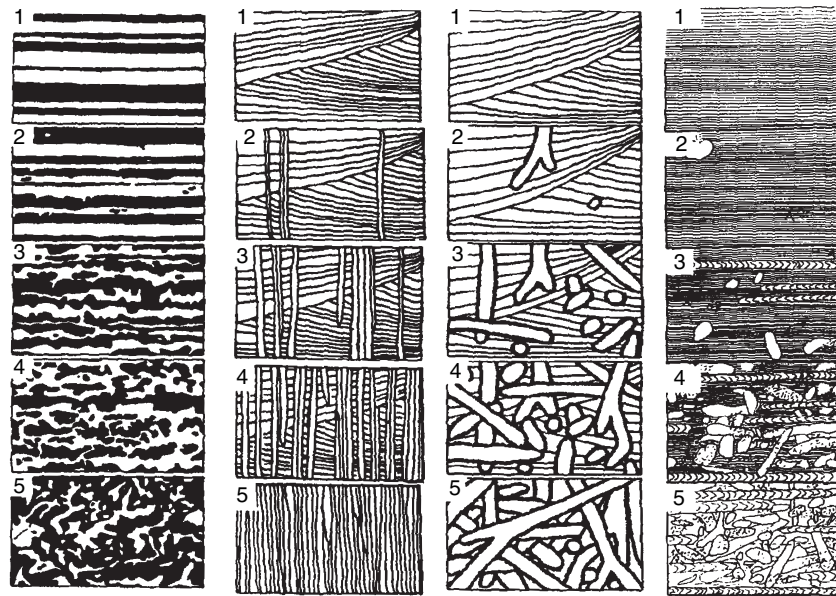


FIGURE 1.20 Ichnofabric index standards for four different environmental settings.

Left to right: shelves; nearshore environments characterized by the vertical trace fossil *Skolithos*; nearshore environments characterized by the trace fossil *Ophiomorpha*; and deep-sea environments. In each setting, higher ichnofabric indices, toward the bottom, indicate a greater degree of bioturbation. (From Droser & Bottjer, 1993)

the fossil record lies in the abundance and diversity of marine organisms with calcitic versus aragonitic skeletons. Because aragonite tends to recrystallize to calcite over time, it is important to note that study of shell microstructure is often able to determine whether what is preserved as calcite was originally calcite or aragonite [SEE SECTION 1.2]. Although the importance of calcite versus aragonite has fluctuated over time, in very rough terms calcitic skeletons are more common in Paleozoic

animals, whereas aragonitic skeletons are more common after the Paleozoic Era.

While the reasons for temporal changes in skeletal composition are still under investigation, the potential importance of aragonite loss can easily be seen by comparing fossil deposits that represent paleoenvironments of the same time and place but that have undergone different styles of diagenesis. In some instances, the more poorly preserved deposits contain aragonitic species as molds only or as recrystallized calcite that has lost most of the original microstructural detail of the shell; the better preserved equivalents contain abundant aragonitic shells. To the extent that calcitic taxa are better represented than aragonitic taxa, the fossil record may prove to be more complete for those intervals of time when calcitic skeletons were truly more common.

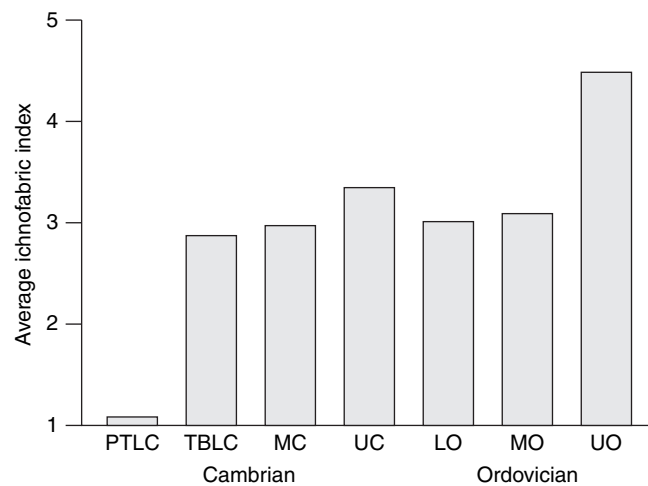


FIGURE 1.21 Average ichnofabric index through the Cambrian and Ordovician, based on a field study of the Great Basin of the southwestern United States. “PTLC” and “TBLC” refer to the pre-trilobitic Lower Cambrian and the trilobite-bearing Lower Cambrian. (From Droser & Bottjer, 1993)

Geographic and Environmental Distribution of Fossiliferous Rocks

Most of the fossil record is marine in origin. It is therefore quite natural that the majority of paleontological research focuses on the marine realm, even if the terrestrial realm is more familiar to many students. Moreover, most of what we know of ancient marine life comes from relatively shallow deposits that were formed when oceans flooded parts of the continents and continental shelves. These deposits have been revealed either by a drop in absolute sea level or by tectonic uplift. Sedimentary rocks deposited in the deep oceans are

sometimes scraped up onto continents at collision zones, and such rocks have also been sampled directly by drilling into the sea floor at great depths [SEE SECTIONS 9.1, 9.5, AND 10.4]. Most oceanic sedimentary rock older than about 180 million years has been subducted, however. The relatively sparse Paleozoic record of the deep seas, compared with that of the Mesozoic and Cenozoic, is the result of subduction of the oceanic crust.

For terrestrial organisms, the most commonly represented habitats are in the coastal lowlands. Habitats at higher elevations are generally in areas of net erosion that are unlikely to be preserved in the sedimentary record for long periods of time. Thus, we have a better record of uplands as we approach the present day.

The global sedimentary record suggests that widespread **epicontinental seas** were more common during much of the Paleozoic Era than they were afterwards. In addition, there has been a general movement of the northern continents (making up present-day North America and Eurasia) from predominantly tropical and subtropical during the Paleozoic to predominantly subtropical and temperate afterwards. As a result of these factors, the relative extent of shallow-marine tropical sediments has generally declined over the course of the Phanerozoic Eon. In contrast to the increasing quantity of the deep-sea record as we approach the present day, however, the general decline in epicontinental seas and the latitudinal shift in continental position are quite real. Geologic evidence shows that tropical, epicontinental seas really were more common in the Paleozoic; it is not the case that we merely have a more complete record of them for that interval of time.

1.5 GROWTH OF OUR KNOWLEDGE OF THE FOSSIL RECORD

As suggested in our earlier treatment of rarefaction, one way to assess the adequacy of the fossil record is to determine at what point the results we have documented no longer change appreciably as we sample more. If a result is stable in the face of improved sampling, we can have some confidence that we are seeing what the fossil record has to offer. Of course, this does not guarantee that we are seeing a faithful reflection of the biological or geological processes we hope to reveal. This is because the fossil record itself may be biased with respect to a particular question; merely increasing the size of the sample is not necessarily going to undo this bias. Moreover,

the principle of diminishing returns means that it may take an enormous amount of additional sampling to add significantly new information to a study—for example, to sample the rarest species.

Sir Alwyn Williams, a specialist on brachiopods, was aware as early as the 1950s that tabulations of the number of taxa known from different periods of geologic time can be idiosyncratic, depending, for example, on the stratigraphic intervals in which particular paleontologists are interested and on the taxonomic concepts that they employ. He therefore conducted a thought experiment: Which stratigraphic intervals would show peaks in the number of brachiopod genera if, at various times in the history of our science, paleontologists had analyzed the data then available? Williams tabulated the number of genera by geologic time period for the data compilation published in 1894 by James Hall and J. M. Clarke, for that published in 1929 by Charles Schuchert and C. M. Le Vene, and for the data available as of 1956, largely the result of efforts by G. A. Cooper and Williams himself.

Successive data compilations are not independent. Instead, they are cumulative, building on previous knowledge and interpretations of fossil material. For example, consider the brachiopod genus *Finkelnburgia*. This genus was erected by Charles Walcott in 1905 on the basis of two species he collected and described from Upper Cambrian sandstones in Wisconsin and Minnesota. Hence, this genus is absent from the 1894 data compilation, but it is listed in Schuchert and Le Vene's 1929 compilation as occurring in the Cambrian. In 1932, Schuchert and Cooper assigned a few specimens from Lower Ordovician deposits to the genus *Finkelnburgia*, and in 1936 E. O. Ulrich and Cooper described several Lower Ordovician species of *Finkelnburgia* from North America. As a result, in the 1956 compilation this genus is present in both the Cambrian and Ordovician.

In fact, the story is more complicated than this. In 1865, Elkanah Billings had described a species from the Lower Ordovician of Canada and assigned it with some uncertainty to the genus *Orthis*. This species, *Orthis? armanda*, was assigned in 1932 by Schuchert and Cooper to the genus *Finkelnburgia*. Thus, material representing Ordovician *Finkelnburgia* was known to paleontologists 40 years before this genus was described and nearly 70 years before it was actually credited to the Ordovician. As this example shows, both the collection of new material and the taxonomic treatment of existing material can affect the inferences drawn from paleontological data.

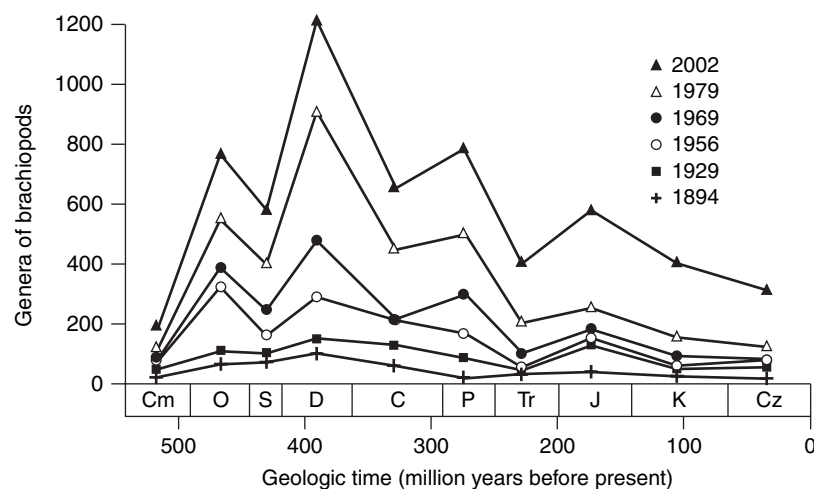


FIGURE 1.22 Genus diversity in brachiopods over geologic time according to six different data compilations, each indicated by its date. The total number of genera known from each geologic period is shown. This figure shows how certain features of evolutionary history start to stabilize as more data are collected. (Data from Williams, 1957; Grant, 1980; & Sepkoski, 2002)

Figure 1.22 shows Williams's tabulations of the total number of genera known from successive intervals of geologic time. The peak in brachiopod diversity for the 1894 data set falls in the Devonian, that for the 1929 data set also falls in the Devonian, but there is a post-Paleozoic peak in the Jurassic; and that for the 1956 data set falls in the Ordovician. Thus, the picture of taxonomic diversity seemed to Williams to be rather unstable, changing in striking ways with additional study.

We can make sense of the particular shifts by taking note of some of the predominant students of fossil brachiopods. James Hall, who was active for much of the second half of the nineteenth century, worked extensively on the Devonian and other Paleozoic rocks of New York State and other areas. Thomas Davidson, a contemporary of Hall, studied Jurassic brachiopods of Europe, but he had what is generally regarded as a conservative, or "lumping," taxonomic approach: He tended to describe forms as new genera only on the basis of rather substantial differences. In the early twentieth century, S. S. Buckman was one of the foremost students of European Jurassic brachiopods. He was more of a "splitter"—he tended to describe new genera on the basis of relatively subtle anatomical distinctions. This helps account for the large number of Jurassic genera in the 1929 data compilation. Finally, by the 1950s, a number of brachiopod specialists had begun to study lower Paleozoic formations in more detail. This helps account for the appearance of the Ordovician peak in the 1956 data set.

A similar study was carried out in 1980 by Richard Grant, who compared brachiopod diversity based on Cooper's 1969 compilation with his own 1979 data set. His results are also graphed in Figure 1.22. The diversity

picture shows some interesting differences compared with the 1956 compilation. For example, the Devonian now appears again as the principal peak, just as it was in the 1894 and 1929 compilations. Moreover, the 1969 and 1979 data sets show a new, subsidiary peak in the Permian. This reflects, among other things, Cooper and Grant's extensive work on the silicified Glass Mountain faunas of west Texas. An important feature of Grant's study is that the 1979 data set, despite being much more extensive than that of 1969, shows essentially the same pattern of diversity over time.

What do the data on brachiopod occurrences tell us today, some 50 years after Williams's study? A 2002 compilation by J.J. Sepkoski [SEE SECTION 8.2], based on that of Grant as well as numerous additional sources, is also depicted in Figure 1.22. This shows that the picture today is actually much as Grant saw it nearly 30 years ago. Overall, there are many more known genera of fossil brachiopods, but the relative distribution of these throughout geologic time appears to have stabilized. Small differences, such as the relative diversity of brachiopods in the Ordovician versus the Permian, are likely to fluctuate slightly as more material is studied. However, major patterns, such as the overall peak in the Devonian and the generally higher level of diversity in the Paleozoic relative to the Mesozoic and Cenozoic, seem to be robust.

Similar studies have been done for diversity in other groups and for many other issues—for example, evolutionary relationships among taxa and the anatomical differences among them. The general outcome of such studies agrees with what has been found for brachiopod diversity: Finer-scale features in the fossil record are more

likely to be overturned as additional data are collected, while large-scale features tend to be stable. However, there is no way of knowing in advance precisely which features will be reliable in any given case. It is therefore important to continue to consider to what extent our interpretations of the fossil record are sensitive to new discoveries.

As illustrated with the example of *Finkelburgia*, comparisons between older and newer data compilations combine two sources of modification: increase in the sheer amount of data and change in the taxonomic opinions and practices of specialists on particular biologic groups. We will discuss taxonomic practice in more detail in Chapter 4. For now, we note that it is possible to isolate this second factor by starting with an existing data compilation and revising it according to a consistent set of taxonomic protocols—for example, how wide a range of species forms to include within a single genus. The

procedure of adopting a consistent approach and scrutinizing existing data to ensure that they are in agreement with the adopted standards is referred to as **taxonomic standardization**.

Figure 1.23 shows some results of taxonomic standardization, in this case, focusing on genus diversity of Ordovician and Silurian trilobites. Part (a) plots the percentage of genera present in the unstandardized data for the given time interval that are not considered valid in the standardized data. This is a measure of the extent of disagreement between unstandardized and standardized data. Parts (b) and (c) depict, for both data sets, total diversity and the percent change in diversity from one interval to the next. It is clear that, despite pervasive disagreements between the two data sets, diversity and short-term change in diversity are actually in substantial agreement. In this example, the discrepancies between the data sets are, in effect, random noise that is averaged out.

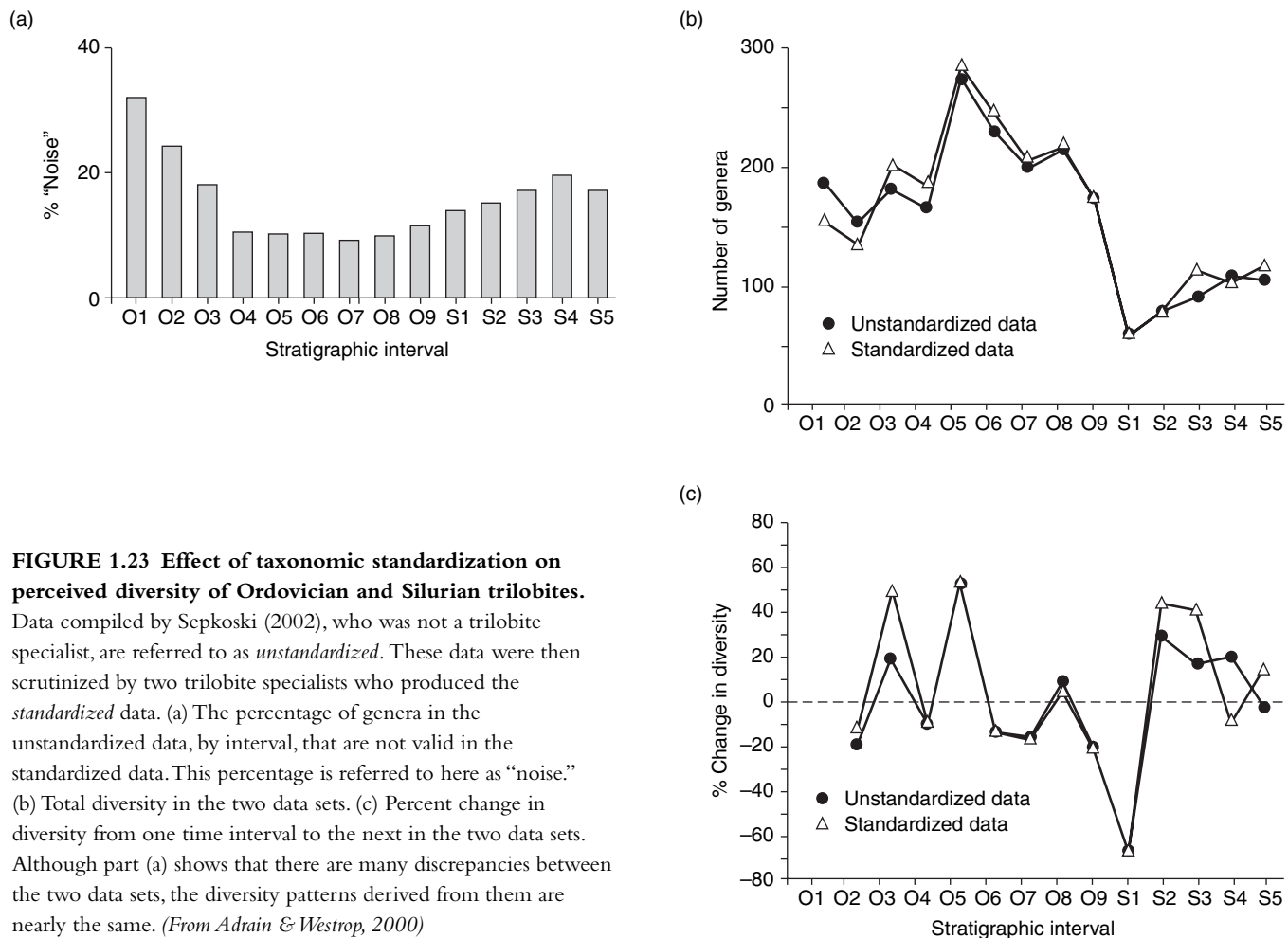


FIGURE 1.23 Effect of taxonomic standardization on perceived diversity of Ordovician and Silurian trilobites.

Data compiled by Sepkoski (2002), who was not a trilobite specialist, are referred to as *unstandardized*. These data were then scrutinized by two trilobite specialists who produced the *standardized* data. (a) The percentage of genera in the unstandardized data, by interval, that are not valid in the standardized data. This percentage is referred to here as “noise.” (b) Total diversity in the two data sets. (c) Percent change in diversity from one time interval to the next in the two data sets. Although part (a) shows that there are many discrepancies between the two data sets, the diversity patterns derived from them are nearly the same. (From Adrain & Westrop, 2000)

1.6 BIBLIOGRAPHIC SOURCES FOR PUBLISHED PALEONTOLOGICAL DATA

The previous discussion of data compilations and how they have grown over time naturally leads to a consideration of how one can keep track of such information. Although we will discuss the mechanics of data compilation throughout this book, a few preliminary comments are in order on the subject of bibliographic sources.

Paleontologic information (particularly taxonomic information) has been published in a vast literature extending back well into the eighteenth century. It is published in all major languages and a wide variety of publication media. Paleontologists are thus highly dependent on bibliographic aids.

Compilation and standardization of data are greatly aided by definitive monographs on either a specific taxonomic group or fossils found in a particular part of the geologic column. If the monograph has been well prepared, it includes reference to all important literature. The reader need then consult other bibliographic sources only for articles that have been published since the publication of the monograph. In using a given monograph, the reader must understand to what taxonomic categories the writer's definitive summary reaches. For example, the authors of the *Treatise on Invertebrate Paleontology*—a summary of the geologic and geographic occurrences, morphology, and classification of fossil invertebrates—attempt to be comprehensive in listing genera but generally do not cover species.

When no up-to-date summary treatment is available, paleontologists must turn to published bibliographies, such as the *Zoological Record*. Each volume is a reasonably comprehensive survey of the zoological and paleozoological literature published during the preceding year. The index includes a comprehensive list of all taxonomic names used in the papers cited. The *Zoological Record* is a valuable aid for a number of areas of work because it permits tracing the bibliographic citations to a genus or species year by year.

The *Zoological Record* is not complete, however. No such bibliography could be and still be issued within a reasonable time after the publication of the literature on which it is based. Therefore, the *Zoological Record* must usually be supplemented by other bibliographies such as *Biological Abstracts*, *GeoRef*, and more specialized sources for particular taxonomic groups.

Electronic bibliographic databases have grown enormously in recent years. These can be rapidly and auto-

matically searched for specified taxonomic, stratigraphic, and geographic terms. Older literature is also incorporated into many such databases. For example, the electronic version of the *Zoological Record* now extends back to 1978, and *GeoRef* goes back to the eighteenth century. Electronic bibliographies have become an indispensable aid to the practicing paleontologist. Despite their great utility, however, all bibliographies are incomplete and imperfectly indexed, and the student should be aware that methods such as cross-referencing and browsing in the library are generally still necessary.

1.7 CONCLUDING REMARKS

The fossil record provides a very small sample of past life. Because so many species have lived in the past and because the amount of time covered is so vast, however, paleontologists have an enormous quantity of data with which to study the history of life. Almost since the beginning of paleontology as a science, a major concern has been how to study biological and geological processes in the face of paleontological incompleteness. In this chapter, we have emphasized two major points:

1. It is possible to design paleontological studies so that the imperfections of the fossil record do not dominate. Major approaches include: (a) focusing on the well-skeletonized fraction of species; (b) comparing fossil assemblages that come from similar environments with similar preservational conditions; (c) using taphonomic controls in order to judge whether the absence of a species from a particular time and environment is likely to be real or preservational; and (d) studying evolution and ecology at a local level, at which the fossil record is relatively complete.
2. Biases in the fossil record can be used to advantage by the paleontologist. An observed pattern that is the opposite of what is predicted by a bias such as differential preservation is likely to be more reliable than one that is predicted by the bias.

To be sure, data from the fossil record cannot always be taken at face value, but available data are often quite adequate for specific purposes. As we will see throughout this book, we can interpret the data of the fossil record in ways that take preservational bias and incompleteness into account.

SUPPLEMENTARY READING

- Allison, P. A., and Briggs, D. E. G. (eds.) (1991) *Taphonomy: Releasing the Data Locked in the Fossil Record*. New York, Plenum Press, 560 pp. [A comprehensive collection of papers on taphonomic processes and the quality of the fossil record.]
- Benton, M. J. (ed.) (1993) *The Fossil Record 2*. London, Chapman and Hall, 845 pp. [A fairly complete survey of the families known from the fossil record.]
- Bottjer, D. J., Etter, W., Hagadorn, J. W., and Tang, C. M. (2002) *Exceptional Fossil Preservation*. New York, Columbia University Press, 403 pp. [Overviews of fossils and geologic features of many of the most important fossil Lagerstätten.]
- Donovan, S. K., and Paul, C. R. C. (eds.) (1998) *The Adequacy of the Fossil Record*. Chichester, Wiley, 312 pp. [A collection of essays on methods and case studies that concern completeness of the fossil record.]
- Pääbo, S., Poinar, H., Serre, D., Jaenicke-Després, V., Hebler, J., Rohland, N., Kuch, M., Krause, J., Vigilant, L., and Hofreiter, M. (2004) Genetic analyses from ancient DNA. *Annual Review of Genetics* **38**: 645–679. [Overview of progress in the extraction and analysis of ancient DNA.]
- Raup, D. M. (1979) Biases in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History* **13**:85–91. [Discussion of some of the more important biases, with particular reference to the tabulation of diversity.]
- Schäfer, W. (1972) *Ecology and Paleocology of Marine Environments* (English translation). Chicago, University of Chicago Press, 568 pp. [Pioneering treatment of actualistic paleontology.]