FOSSIL RECORD

There are more than 1.5 million named and described species of plants and animals on Earth, and probably, many more exist that have never been identified. Some estimates place the total number at approximately 4.5 million species, yet the fossil record preserves only a small fraction of this total and does so in a very selective manner. Some groups of organisms with hard parts (such as shells, skeletons, or wood) tend to fossilize readily; therefore, much is known about their past. Many others are soft-bodied and rarely, if

ever, fossilize, so paleontology has little to say about their history. The study of how living organisms become fossilized is known as taphonomy (Greek for "laws of burial").

The Completeness of the Fossil Record

It is interesting to gain an appreciation of how unlikely the process of fossilization can be. For example, modern biological studies

have revealed that the typical sea bottom is often dense with shells. In a study conducted on one-quarter of a square meter of seafloor off the coast of Japan (Thorson 1957), the shell count yielded 25 individuals of a large bivalve (Macoma incongrua), 160 of a smaller cockle shell (Cardium hungerfordi), and 12 of the tusk shell (Dentalium octangulatum). The average age of these molluscs was found to be two years. At this rate of deposit, there would be an accumulation of 1,000 shells in just 10 years, or 100 million shells in a million years—over one-quarter of a square meter thick. If this figure is extrapolated for the entire seafloor over geological time, it suggests that a staggering number of shells could have been fossilized. In fact, the tiny area of seafloor near Japan could produce more fossilized shells than actually are known from the entire fossil record. Clearly, most organisms do not become fossils.

Is it possible to determine in numerical terms the accuracy of the fossil record? We have already estimated that there are 1.5 million described species, or as many as 4.5 million described and undescribed species of organisms alive on Earth today. How many species are known as fossils? There are only about 250,000 described species of fossil plants and animals presently known, translating to just 5 percent of the total number of species living today. But, the present is only one moment in geologic time. If we multiply the present diversity by the 600 million years that multicellular life has existed on the planet, the estimate grows considerably. No matter how one does this calculation, it is clear that the quarter of a million species known as fossils represents only a tiny fraction of a percent of all the species that ever lived.

About half of the 1.5 million described species are insects, which have a poor fossil record and are not useful in estimating the total number of species. Let us just focus on nine well-skeletonized phyla of marine invertebrates and see if we come up with better estimates. These nine phyla are the Protista, Archaeocyatha, Porifera, Cnidaria, Bryozoa, Brachiopoda, Mollusca, Echinodermata, and Arthropoda (excluding insects). Among these groups, there are about 150,000 living species, but more than 180,000 fossil species. To translate these numbers into an estimate of the completeness of the figures, the paleontologist must know the turnover rate of species and the number of coexisting species through time. Different values have been used for each of these variables, but the results of the calculations remain remarkably similar. No matter which values are applied, it appears that 85 to 97 percent of all the species in the nine, well-skeletonized phyla that have ever lived have never been fossilized.

This is a very sobering estimate. It forces us to step back and reassess the limitations of almost any study based on fossil data. However, there is another consideration to bear in mind: The quality of the record depends on the level of detail we require. For a census of all the phyla or classes of invertebrates in a given sample, it would not be hard to get a complete sample. Obtaining every species is much harder, for the simple reason that a higher taxon, like a phylum or class, contains many different genera and species. If we obtain one species in each given phylum or class in a sample, we have a complete sample of phyla or classes with only a few specimens. But we need huge samples to get every species, or even every family or genus, that might have lived in a given time and place.

Fossilization Potential

To understand and interpret the preserved fossil record, the paleontologist must first determine how taphonomic processes have biased a sample. From the moment an organism dies, there is a tremendous loss of information as it decays and is trampled, tumbled, and broken before it is buried. The more of that lost information that we can reconstruct, the more reliable our scientific hypotheses are likely to be. Every paleontologist therefore must act as a coroner-forensic pathologist-detective to determine how the victim died and attempt to reconstruct the events at the "scene of the crime."

Numerous studies have documented the biases inherent in the processes of death and decay and have estimated the preservation potential of various marine invertebrates. For example, three different studies independently concluded that 25 to 30 percent of the species are likely to be preserved in the fossil record, with snails and clams having the highest potential. The soft-bodied groups, such as flatworms, segmented polychaete worms (which may make up 40 percent of the species in modern shallow marine habitats), and other wormlike organisms have very little chance of fossilization. Some arthropods (such as heavy-shelled crabs and barnacles) may fossilize, but other thin-shelled crustaceans, such as shrimp, rarely do. A few thick-shelled echinoderms, such as sea urchins, fossilize, but sea stars and brittle stars have little chance of becoming fossils.

After a death assemblage accumulates, many other factors operate on the hard parts to break them up and scatter them around, so an even smaller percentage ends up buried for future fossilization. These agents of destruction can be biological, mechanical, or chemical.

Among the forces of destruction, biological agents are the most important factor in most environments, both marine and terrestrial. Predators and scavengers are very active in breaking up shells and bones to extract almost all the useful nutrition from them. On the seafloor, a variety of organisms (especially fishes, crabs, and lobsters) are effective in cracking shells to extract their food content. In addition to such activity on the part of predators and scavengers, the shells themselves are subject to other biological agents of destruction. The most important of these are organisms that use the shell as a substrate (surface on which to live) or source of food or nutrients. A variety of organisms-including boring algae, boring sponges, worms, and bryozoans-erode holes and canals in dead shells and eventually weaken them so that they fall apart.

On land, a variety of predators and scavengers work very quickly to break up carcasses or vegetation. Once a tree falls in the forest, a wide variety of organisms—from termites, ants, beetles, and worms, to fungi and bacteria of various kinds-reduce it to organic material that can be recycled back into the food chain. In the African savanna, for example, a wide spectrum of scavengers (from jackals, hyenas, and vultures) and decomposers (insects and bacteria) quickly reduce most carcasses to nutrients that the soil can absorb. The key factor that prevents biological destruction is rapid burial.

Mechanical agents of destruction such as wind, waves, and currents can be very important. These processes are most effective in shallow waters where both waves and storms achieve their greatest force. The densest, most fine-grained shells are the most durable, but skeletons with coarsely crystalline structures (such as oysters) or porous structures (such as corals) are less durable, even if they are relatively thick. The shape, density, and thickness of the bone or shell are the most important factors in determining whether it can withstand the mechanical transport of waves, storms, or river currents.

After burial, a variety of chemical agents and diagenetic changes (i.e., changes after burial) in the rock (especially metamorphism) easily can destroy the shells and prevent their preservation. For example, aragonitic fossils are much more prone to dissolve than calcitic fossils, so fossils that are made primarily of aragonite are discriminated against in the fossil record. One study censused a living oyster bank and found over 303 species (mostly soft-bodied worms). Of the shelly invertebrates, 16 percent (nearly all the snails and many of the bivalves other than oysters) had aragonitic shells. Looking ahead, once these had dissolved, the remaining "oyster community" would appear to be of low diversity, because only these species with calcitic shells would be fossilized. This would be a false conclusion. The original composition and groundwater chemistry are the most important factors in determining whether diagenetic changes are likely to alter or dissolve a fossil

Finally, only a small portion of all the fossiliferous rocks in the world have been exposed during the last few centuries, when people began to collect them. An even smaller proportion of these outcrops have been seen by a qualified collector before the fossil erodes and is destroyed completely. The chances of a given animal having the extraordinary luck of not only being preserved but also of being collected by a paleontologist are extraordinarily small.

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See also Fossilization Processes; Fossil Resource Management; Geological Timescale; Mortality and Survivorship; Sedimentology; Taphonomy; Trace Fossils

Further Reading

Behrensmeyer, A.K., and A. Hill (eds.). 1980. Fossils in the Making. Chicago: University of Chicago Press.

Paul, C.R.C. 1982. The adequacy of the fossil record. In K. Joysey and A.E. Friday (eds.), Problems of Phylogenetic Reconstruction. New York and London: Academic.

Prothero, D.R. 1998. Bringing Fossils to Life: An Introduction to Paleobiology. Boston: Brown/McGraw-Hill.

Raup, D.M. 1976. Species richness in the Phanerozoic: A tabulation. *Paleobiology* 2:279–88.

Shipman, P. 1981. Life History of a Fossil. Cambridge, Massachusetts: Harvard University Press.

Thorson, G. 1957. Bottom communities (sublittoral or shallow shelf). Geological Society of America Memoir 67:461–534.