THE NATURE OF THE FOSSIL RECORD

SUSAN KIDWELL
and
J. JOHN SEPKOSKI, JR.

Department of the Geophysical Sciences
University of Chicago
5734 South Ellis Avenue
Chicago, Illinois 60637

INTRODUCTION

The term "fossil record" is used in two ways: either the totality of fossils preserved in all rocks or the sum of human knowledge of those fossils. In either case, the term carries the connotation also of the geologic context of the fossils—their distribution in time and space and their relationship to the enclosing rock. One of the primary scientific interests in the fossil record is learning about the history of life and the processes of large-scale transformation, or evolution, in the forms, diversities, and biological interactions of life.

Learning from the fossil record can be likened to reading an ancient manuscript composed over many generations. The youngest pages are reasonably complete, but the older pages are crumbling and are written in an increasingly archaic language; supplemental texts are needed to interpret much of the older parts of the decaying manuscript.

In this chapter, we briefly discuss the nature of the immensely valuable and complex manuscript that is the fossil record—how it is discovered and analyzed, its strengths and weaknesses, and some of the information that can be read from it.

WHAT ARE FOSSILS?

Fossils can be considered as any trace of ancient life preserved in natural geological deposits. Although fossils as ancient life had been recognized for many centuries, Steno first articulated the criteria for recognizing fossil organisms in 1669, with specimens we now recognize as shark teeth of Pliocene age (see Gould, 1981). Steno began by reasoning that an object within a rock must be older than the encasing sediment. He then set out criteria for organic origin: if the specimen removed from the rock looks like a modern shark's tooth, not just superficially but in many details, if it has the same internal structure, and if it also has the same composition, then the most logical conclusion
other groups having more prolonged, and therefore less informative stratigraphic ranges, are fitted into the framework by their positions in the rocks with respect to the index fossils and other indicators of geologic time and correlation. Most fossils in fact have evolutionary durations that are too long to be used as index fossils, or are too sensitive to environment conditions to be found in a sufficiently large array of sedimentary rock types or range of latitudes to correlate rocks globally.

Given these complexities of the sedimentary record, it is reasonable to ask whether the quality of the fossil record is adequate for evolutionary analysis. One problem of particular concern is that the rock record of the oldest intervals of geologic time, such as the "Precambrian," tend to have less complete sedimentary records than younger intervals. This is because of greater elapsed time for rocks to be destroyed by tectonic uplift and erosion, for metamorphic erasure of original fossil and rock features, etc. In fact, many areas of the Earth preserve no early record of geologic time (and no area preserved a record older than 4.0 Ga, despite a well-accepted age of the Earth of 4.6 Ga based on astronomical evidence for the age of our solar system). The "Precambrian" encompasses in fact about 90% of all recorded geologic time, but rocks of this interval constitute less than 10% of preserved sedimentary rocks (by volume). The older phases of geologic history (and thus of the history of life) are therefore based on less information gleaned directly from the fossil record, largely because fewer rocks are preserved from these early periods.

The analogy with libraries applies here, also: There are geographical differences in the degree of development and maintenance of libraries (their completeness), greater wear and tear on the oldest holdings within any given library, and fewer libraries in existence during the earliest phases of book production.

Notwithstanding the secular trend in rock preservation, geologists can piece together a remarkably complete and high-resolution series of master columns at regional and global scales through careful correlation. With the combination of the advent of higher resolution methods of correlation and absolute dating, continued field work in new areas, and the development of computerized databases, the known geological framework for discovering and analyzing the fossil record is becoming increasingly complete and refined. (The analogy might be to what librarians can now do with web links to other libraries--missing issues of even the most obscure journals and newspapers can be tracked down for local readers, and key-word databases allow even contents to be searched more effectively.)

Modern methods and the accrual of field discoveries have thus revolutionized our quality of information on the rock record and the framework for evolutionary studies since the mid-19th century. The rocks have not changed, nor the fossils they contain. But our knowledge of their ages, geographic distribution, and origins has been greatly enhanced.

SO HOW BIG [AND COMPLETE] A FOSSIL RECORD DO WE HAVE?

The answer to this question involves both bad news and good news. Let's begin with the bad news, performing a simple calculation. The results will not be exact, but they will provide a "ballpark" figure for what percent of animals that ever lived in the oceans
have been found as fossils. Animals in the oceans are used because numbers for them are best, but the results are instructive for the entire fossil record.

To determine what percent of ancient marine animals ( multicellular metazoans) have been discovered, we need four numbers:

1. The actual number of fossil species described: This is approximately 200,000, based on a count by Raup (1976).

2. The number of animal species in the oceans today: This is unfortunately poorly known, but best estimates place it around the same number, 250,000 species (or $2.5 \times 10^5$).

3. The age of the oldest animal species: There is debate about this, but the oldest age of unambiguous metazoan fossils is about 600 Ma (given some rounding for simplicity).

4. The average duration of a marine animal species: Raup (1991) estimated this to be about 4 myr; of course, many species existed for a much shorter time whereas some existed much longer.

The final piece of information necessary for the calculation is how the diversity of species has changed from 600 Ma to the present. This is difficult, but we will take two shortcuts. First, we will assume that the record for higher taxa, specifically taxonomic families, is a good proxy for species. Data for the history of fossil families are much better than for fossil species (because families are more inclusive groups and thus more likely to have at least one member represented), and comparative studies indicate that families parallel the diversity of species in a general way. The diversity of fossil families in the oceans since 600 Ma is illustrated in Figure 3 (top of page 70).

The second shortcut will be to simplify the history of family diversity. That history is irregular, but very interesting. However, note that if a straight line is drawn from the known diversity at 600 Ma to the known diversity at present, the area above the line is approximately equal to the area below; that is, the error cancels out (Fig. 3). Using this, an estimate of how many animal species that have ever lived in the oceans can be made by calculating the area of the right triangle in 4 myr intervals:

$$\frac{1/2 \times (2.5 \times 10^5 \text{ species}) \times (600 \times 10^6 \text{ years})}{4 \times 10^6 \text{ years}}$$

$$= 18,750,000 \text{ species (or approximately } 188 \times 10^5 \text{)}$$

Thus, the percentage of fossil species of marine animals that have been described is:

$$100 \times \frac{2.5 \times 10^5 \text{ species}}{188 \times 10^5 \text{ species}} = 1.3\%$$

This small percent looks very much like bad news. But actually, we can not expect all groups of animal species to be preserved. In fact, about two-thirds of animal species in the oceans today have no mineralized hardparts. So if we consider just the animals that
today have a reasonable chance of becoming fossils, the rough estimate of the completeness of the fossil record becomes something like 4%.

Figure 3. Known (observed) diversity of marine metazoan families (multicellular animals; stippled line) through the Phanerozoic (adapted from Sepkoski, 1985).

A 4% sample still sounds very small. However, compare it to the sizes of sociological samples, such as the Gallup Pole and Nielsen Ratings; those sample sizes are a small fraction of 1% of the U. S. population. In comparison, knowledge of 4% of potentially fossilizable species is huge. Yet it must be realized that this means that for any known fossil species, there is only a 4 in 100 chance that its direct ancestral species will also be known from the fossil record. (A different approach using simulations yields an estimate of 8 in 100, which is in the same ballpark; Foote, 1996).

These numbers are rough and represent only averages. Some taxonomic groups are much better represented in the fossil record and have engendered much more study. For example, articulate brachiopods all have calcite shells and are often useful for biostratigraphic and paleoenvironmental analysis; knowledge of their history seems to be fairly complete (Foote and Sepkoski, 1999). Sponges, on the other hand, have skeletons
that consist of very small spicules of various compositions—calcite, aragonite, silica, and collagen—and are not used in biostratigraphy; knowledge of their history is consequently much more meager.

So how good is good? One way paleontologists estimate the completeness of the fossil record is by studying the preservation-potential of modern organisms, using these as a "modern analog" for extinct ancestors. Among marine mollusks, for example, we find that, on average, ~90% of species sampled alive in a habitat are represented by dead shells in the top few inches of the seafloor in the same habitat; if we compare the composition of living mollusk communities with the local Pleistocene record, we find ~80% agreement in species' presence (see review by Kidwell and Flessa, 1995). Mollusk shells thus have quite high potential for preservation, at least in the first ~1 million years of their burial history. The few live/dead comparisons that have been conducted for other groups indicate lower but still quite high agreements: for example, 76% among Red Sea echinoids (sand dollars, sea biscuits), and 72% among East African land mammals >1 kg body weight (op cit.). The quality of the fossil record of the most commonly studied fossil groups, all of which have mineralized skeletons and high preservation potentials, should thus not be judged by the improbability of finding a fossil jellyfish or earthworm.

**BROAD PATTERNS OF HISTORY IN THE FOSSIL RECORD**

The sample of known species from the fossil record may be small, but it grows as one proceeds up the taxonomic hierarchy: it takes but one species to document a genus, one genus to document a family, and so on. Thus, taxa above the species level are often used to examine knowledge of the fossil record and to analyze large-scale patterns in the history of life. Figure 4 summarizes our present state of knowledge of family-level diversity through the Phanerozoic for both marine and continental organisms (marine includes both invertebrate and vertebrate animals; continental includes both land plants and animals).

![Figure 4](image_url)

*Figure 4.* Family-level diversity of marine and continental organisms, showing a strong overall increase through the Phanerozoic, and the increase in our knowledge of diversity from 1982 (lower line in each diagram) to 1992 (upper line).
Figure 5 (pages 73-74) presents more detailed information on how these families are distributed among major groups of organisms through the Phanerozoic (the last 545 myr of geologic time) (Sepkoski and Hulver, 1985). These “spindle diagrams” are based on compilations by taxonomic experts using information from around the world. One set of spindles is for marine families, and the other for terrestrial families. Both the detailed data in Figure 5, and the "summed" data in Figure 4, show two interesting features that still fuel debate among paleontologists:

1. The diversity of complex life has grown toward the present and has reached its highest levels near the Recent (which stretches back to 10,000 years ago).

2. The growth of diversity both in the oceans and on land has not been constant but rather marked by abrupt radiations, intervals of constancy, and massive extinctions.

Understanding of these very general patterns really requires analysis of the histories of the taxa that contribute to it. The widths of the spindle diagrams in Figure 5 show recognized diversity at geologic intervals (mostly stratigraphic stages, averaging about 7 myr in duration). However, the data have been “ranged through,” meaning that a taxon, such as ctenophores (“comb jellies”), that is rarely preserved in the fossil record but alive today, is show by a thin line from its last (sometimes only) known fossil occurrence to the Recent. The more common and readily preserved taxonomic groups, such as articulate brachiopods and snails, have much more of the intricacies of their histories recorded in the fossil record.

The spindle diagrams show that a great deal of interesting history is known, despite having sampled only a small percent of species. A major activity of paleontologists and evolutionary biologists continues to be search for a fuller understanding of this variety of histories. The spindles representing different groups expand and contract at different rates and different times, although they sometimes behave in concert, as in the great mass extinction at the end of the Mesozoic Era. Based on what we can infer about the life habits of certain groups in the geologic past, the reciprocal expansion and contraction of some groups may represent interactions among some groups. For example, expansion of predatory arthropods and seastars, or of potential competitors among the bivalves, may have caused the decline of brachiopods. Such ideas can be tested using additional lines of evidence, such as the reconstructed ecologies of ancient seafloor communities.

Thus the fossil record, although incomplete, is a remarkably rich document of the history of life that can be used in myriad ways, from the correlation of oil-bearing rocks to the tracing of evolutionary changes over great expanses of geologic time. Because we are learning to recognize and understand many of the gaps and absences in that record, we can ask questions about the history of life in far greater detail, and with greater scientific rigor, than ever before.
Figure 5. "Spindle diagrams" summarizing known diversity of marine organisms within major taxonomic groups from the Precambrian (Po) through the Cenozoic (Cz) as of 1982 (adapted from Sepkoski and Hulver, 1985).
Figure 5, cont. "Spindle diagrams" summarizing known diversity of continental organisms within major taxonomic groups from the Precambrian (Pc) through the Cenozoic (Cz) as of 1982 (adapted from Sepkoski and Hulver, 1985).
REFERENCES CITED


