CHAPTER 9A

PALEOBIOLOGY

PART I. PRECAMBRIAN LIFE

1. INTRODUCTION

1.1 Life on Earth began early. The oldest undoubted fossils are about 3500 million years old, back in the early Archean—and, as you will see in a later section of this chapter, the earliest fossil organisms are very similar to organisms that are abundant and successful today. These organisms, although primitive compared to advanced metazoans (like us), are, in an absolute sense, rather advanced in their physiology. It's generally agreed that the earliest life, earlier than that represented by the oldest fossils, must have been much simpler and less sophisticated biochemically The clear implication is that *life must have evolved much earlier than 3.5 Ga—*although it is doubtful if fossils much older than that will ever be found. Why not? Perhaps largely because the sedimentary rocks in which they would have been preserved are no longer around, in pristine, unmetamorphosed condition, for us to scrutinize.

1.2 This section purports to tell you something about the nature and evolution of life in the Precambrian (more specifically, up to the latter part of the Proterozoic; for the rise of eukaryotic organisms in general, and multicellular eukaryotes in particular, late in the Proterozoic, see the following section). For the sake of full disclosure here, I should point out that I am a novice in biology! I feel myself to be especially inadequate when it comes to the biochemistry of metabolic process and the molecular biology of replication and inheritance. With that disclaimer, however, I have attempted here to present to you the basics of the fossil record of the Precambrian and some of its implications for the early evolution of life. If you have a special interest in paleontology, and in particular the earliest life you might consider going into the literature. I have provided a fairly long list of materials, largely review papers by specialists in the field.

1.3 Just to set the stage at this early point in the chapter, Figure 9-1 is a diagram that shows, in a very generalized way, the known distribution of stromatolites and microbial microfossils through geologic time. The clear message from Figure 9-1 is that *the Archean fossil record is scanty but real, and the Proterozoic fossil record is far more abundant*. The terms used in Figure 9-1, as well as some of the place names, will be elaborated later in this section.
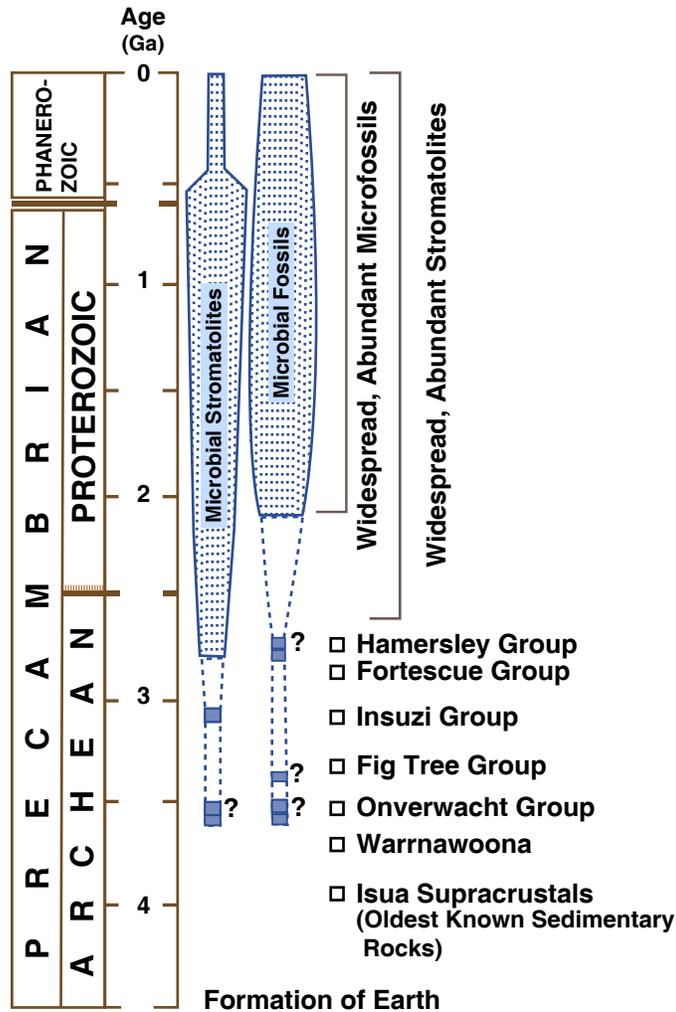
Figure by MIT OCW.

Figure 9-1: Diagram showing the known distribution of stromatolites and microbial rnicrofossils through geologic time

2. THE KINGDOM OF LIFE

2.1 Back when I was a child, the standard idea was that life was divided into the plant kingdom and the animal kingdom. (In fairness to biologists, I should point out that the experts knew then that the situation was more complicated: what to do about fungi, for example?). Progress on deciphering the "tree of life" (that is, the evolutionary development of the various life forms known today, through geologic time, from a presumably common original ancestor) has been truly spectacular in recent years. With the development of techniques for

examining the genetic material carried by RNA and DNA, it is now possible to trace evolutionary lineages back in time. (I would have included a "background section" on that, but I think that it would have taken me weeks, not just days, to produce an adequate one, given the very steep learning curve I would have faced.) Biologists now have a fairly generally accepted picture of the "tree of life". Before considering that, however, we need to deal with some rather intricate terminology for organisms and their metabolic processes.

2.2 The basic distinction among organisms is between *unicellular organisms* and *multicellular organisms*. Among the unicellular organisms, there is another fundamental distinction: between *prokaryotes* and *eukaryotes*. Prokaryotes are relatively primitive unicellular organisms in which the protoplasm and the genetic material are encased within a cell wall of some kind but the genetic material is not located within a nucleus. Eukaryotes are relatively advanced unicellular organisms in which the genetic material is enclosed in a special nucleus within the cell. Prokaryotes reproduce asexually, whereas eukaryotes reproduce sexually. (The implication of that is that the pace of evolution was very slow early on, but quickened with the advent of eukaryotes, because sexual reproduction allows the ever-arising mutations to spread rapidly through an interbreeding population, leading to Darwinian evolution through natural selection processes.) The earliest fossils are believed to be prokaryotic; eukaryotic organisms evolved in the course of the Proterozoic.

2.3 All organisms can be classified as either *heterotrophic* or *autotrophic*. A heterotrophic organism obtains its raw-material energy resources (its "food") from preexisting organic matter (or abiotic organic molecules). An autotrophic organism synthesizes its own organic materials by conversion of simple inorganic compounds, making use of a variety of external energy sources.

2.4 There seems to be a general consensus that *the very earliest organisms must have been heterotrophs*, because heterotrophs can be simpler in their metabolic processes than autotrophs. In that view, the more advanced autotrophic life forms evolved from early heterotrophs. The problem with widespread heterotrophy is that eventually the organisms use up whatever stock of "food" is available, and without autotrophy, no more "food" is produced—except perhaps by the continuing inorganic synthesis of abiotic organic molecules, which would not have been produced in any great abundance.

2.5 Depending on the form of energy utilized, autotrophs can be classified as either *chemoautotrophic* or *photoautotrophic*. Chemoautotrophic organisms use chemical energy to fuel their processes of biochemical synthesis. Such organisms are known to exist today, perhaps most spectacularly in the deep ocean, in the vicinity of hydrothermal vents (called, picturesquely, "black smokers") associated with mid-ocean spreading ridges. Photoautotrophic organisms use solar energy for their processes of synthesis.

2.6 Photosynthesis is a complex set of biochemical processes. The basic nature of all photosynthesis is to start with some relatively reduced compound that's stable in the natural environment, and oxidize it using solar radiation as the source of the needed energy to drive the reaction, and using certain compounds, like chlorophyll, as catalysts to enable the reaction to happen. The general reaction can be written as

$$CO_2 + 2H_2X + \text{light energy} \rightarrow (CH_2O) + H_2O + 2X$$

The representative of element "X" in this reaction that is most familiar to you is, of course, oxygen: by photosynthesis, the organism splits the water molecule (which takes a lot of energy) and combines the hydrogen released with carbon dioxide to manufacture carbohydrate cell material (represented here by the simplest form of carbohydrate; the carbohydrate sucrose, heavier but still simple, has the molecular formula $C_6H_{12}O_6$) and free molecular oxygen. That's called oxygenic photosynthesis (and the organisms that do it are called *oxygenic photoautotrophs*). Many organisms do not have chlorophyll and so can't use oxygen for the "X" in photosynthesis. Many bacteria contain compounds catalytically similar to chlorophyll that enable them to use H_2S, hydrogen sulfide, as the raw material. That kind of photosynthesis, called *anoxygenic photosynthesis*, produces free sulfur rather than oxygen as the by-product. The organisms that do this are called *anoxygenic photoautotrophs*.

2.7 Now for the main show of this section. Figure 9-2 is a diagram that shows, schematically, the "tree of life" (which is more properly called a ***phylogenetic tree***—that is, how the major taxa of organisms have developed through time) as it was understood in the early 1990s. (I have not discovered a more recent version.)
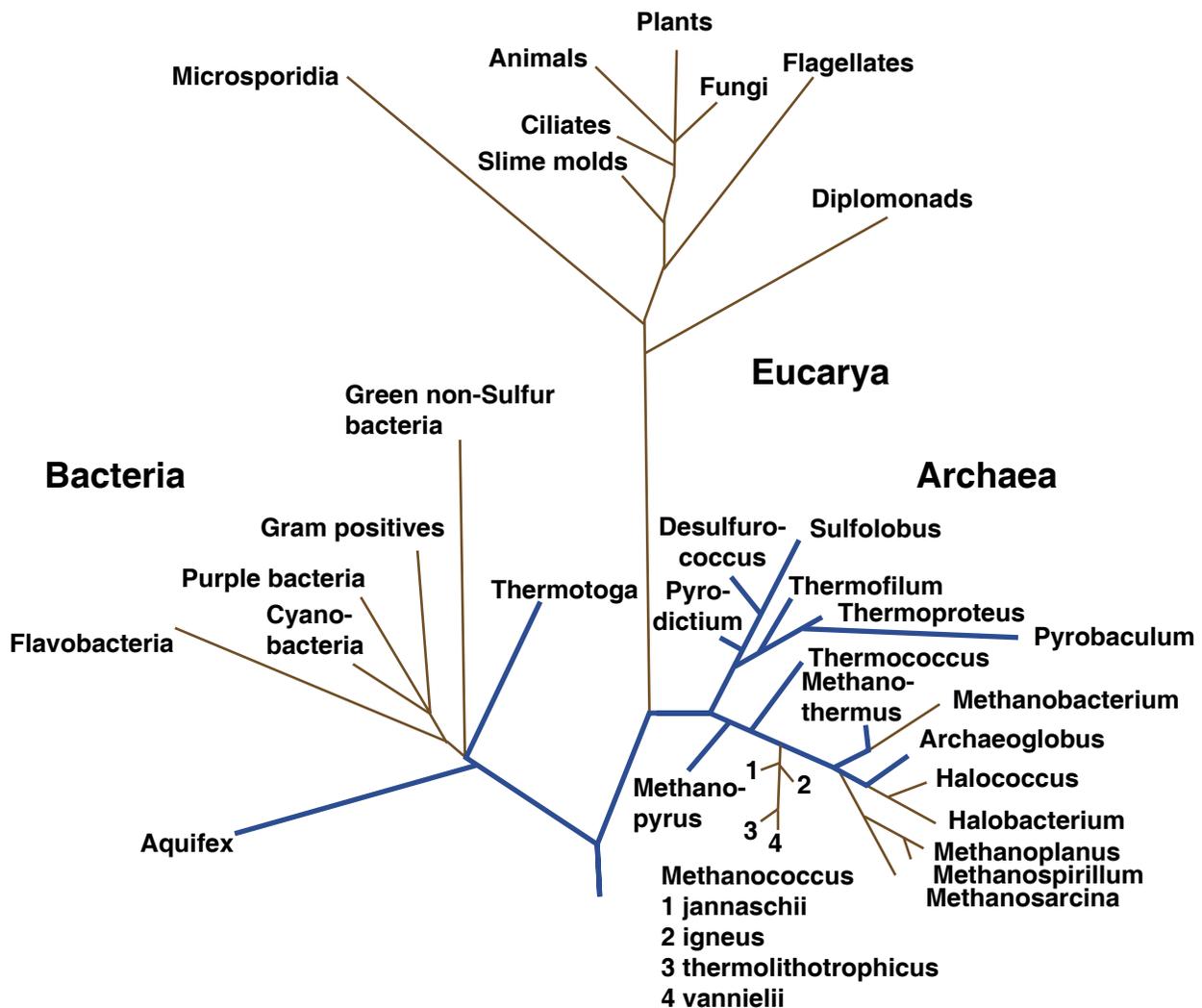
Figure by MIT OCW.

Figure 9-2: The universal phylogenetic tree. The bold lines are hyperthermopluiles

2.8 Biologists now agree that there are three fundamental domains of life: *eubacteria* (formal name: Bacteria); *archaebacteria* (formal name: Archaea); and *eukaryotes* (formal name: Eucarya). This was generally known well before the breakthrough in use of techniques of molecular biology to pin down the phylogenetic tree, but the structure of the tree was not well known. All of the "branch tips" shown in Figure 9-2 are represented by living organisms: that's what makes it possible to trace the lineages back in time. In Figure 9-2, there we are, up along the top, having branched off one of the four major lines of eukaryotes, at about the same time as plants and fungi. Is it some consolation that we are more closely related to slime molds than to bacteria?

2.9 The big mystery in a diagram like that in Figure 9-2 is, of course: *what was the common original ancestor, represented by the open line at the bottom of the diagram?* It's extremely unlikely that we will ever find any direct fossil evidence of it in the early geologic record. Another very interesting feature of the phylogenetic tree in Figure 9-2 is that *all of the earliest life forms seem to have been hyperthermophilic*. As the term implies, a hyperthermophilic organism is one that *loves extremely high temperatures*, even greater than 100°C. They are

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known from a variety of extreme Earth environments today, and they are all very primitive prokaryotes, both eubacteria and archaebacteria. It's possible, of course, that one or more "deep" branches of the tree became extinct early on. If so, we can't include them in this tree. And, of course, if in addition they left no fossil record, we know nothing about them at all!

2.10 Figure 9-3 is a version of Figure 9-2 that shows not only the phylogenetic tree but also a lot of information on the nature of photosynthesis, in the cases of photosynthesizing organisms. What's striking, to me, about Figure 9-3 is that *both modern multicellular plants and cyanobacteria engage in oxygenic photosynthesis* and, more specifically, *use the same details of chemical processes in photosynthesis* (the so-called Calvin–Benson cycle; no details here). Cyanobacteria are an ancient kind of eubacteria, formerly called blue–green algae, but now known not to be closely related to true algae. They are widespread and important in today's world as well—and their nature seems not greatly different from their representatives in the earliest fossil record (see a later section). The implication is that their pace of evolution has been extremely slow.
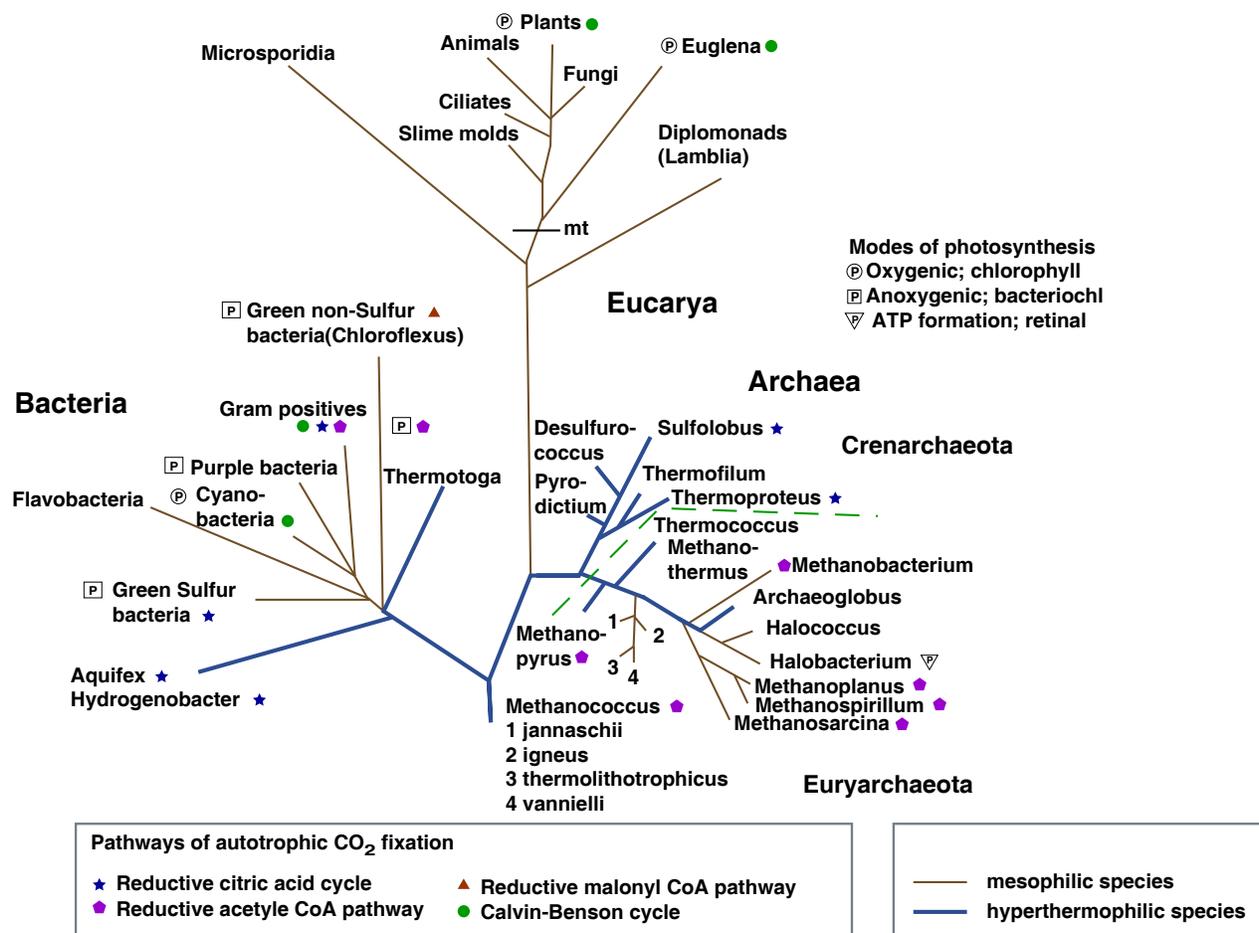
Figure by MIT OCW.

Figure 9-3: The universal phylogenetic tree, with information on photosynthetic processes

3. THE NATURE OF FOSSILS

3.1 What is a Fossil?

3.1.1 A *fossil* can be defined, broadly, *as any evidence of past plant or animal life contained in a sediment or a sedimentary rock*. The word comes from the Latin *fossilis*, an adjective meaning "dug up". In the early days of geology, the term was applied to any interesting natural object (minerals; pieces of ore; pieces of rock; traces of life) that were, literally, dug out of the ground. The term gradually came to be restricted to materials that give evidence of past life.

3.1.2 (One qualifying note at this point, though: the mere presence of disseminated organic matter in ancient rocks, which might technically fall under the definition of a fossil above, is excluded by tacit agreement. And the average concentration of such organic matter in sedimentary rocks is surprisingly high, something like one to two percent. More later in the course on the role of that organic matter in our energy-hungry modern society.)

3.1.3 There are two kinds of fossils: body fossils and trace fossils. **Body fossils** are *the actual organism or some part of it, or the imprint of the organism or some part of it*. Even more abundant than body fossils, however, are **trace fossils**, which are *physical evidence of the life activities of now vanished organisms*. Tracks, trails, burrows, feeding marks, and resting marks are all trace fossils. Trace fossils are useful for geologists and paleontologists because certain kinds of organisms, which live in specific environmental conditions, make distinctive traces. When you hear the word "fossil", you might think of shells or dinosaur bones. These are indeed good examples of body fossils, but there are many other kinds of fossils, including both body fossils and trace fossils.

3.1.4 In relatively young sediments and rocks, the actual body parts of organisms are often preserved. In older rocks, however, the body parts are usually dissolved away, or recrystallized, or replaced by another kind of mineral. Even so, the imprints of the organisms are still preserved, and they can be studied if the rock splits apart in the right place and the right orientation to reveal the imprint. Paleontologists usually collect large numbers of rock pieces and then split them in the laboratory with special mechanical splitting devices to try to find at least a few fossils.

3.2 Fossilization

3.2.1 Two important things to remember about the fossil record are that *it's imperfect* and it's *biased*. Something like a quarter of a million fossil species have been discovered and described. This represents only a small percentage of the million and a half species known to be living today. There are certainly a lot more fossil species yet to be discovered, but by the same token probably only a third of the species in existence today have been recognized and described so far. But things are not as bad as they might seem, because almost half of today's species

are insects, and only a few thousand fossil insects species are known, because of the difficulty of preserving insects in the fossil record.

3.2.1 It is clear that some organisms are readily preserved and others are seldom, if ever, preserved. Organisms with robust hard shells composed of difficultly soluble material, like calcite, are readily preserved if the shells are buried permanently soon after death of the organism. For the body of an organism to become preserved as a fossil, it must escape destruction, at least in part, both before and after it is buried with sediments. Destruction before burial might result from chemical and/or biological decomposition, or from mechanical effects like abrasion and/or breakage during transport by wind or water currents, or a combination of both. (Fragments produced by breakage and abrasion during transport are among the major constituents of limestones. Technically, such particles are fossils, and sedimentologists tend to call such stuff "fossil fragments", but they are not beloved of paleontologists because they are not very suitable for figuring out details of body morphology.) Soft-bodied organisms like worms and jellyfish become preserved only under special circumstances, when their freshly dead bodies come to rest in soft, fine mud and are buried immediately. There is a very high probability that any organism on Earth will be either consumed by another organism or decomposed by microorganisms following death. *For an organism or body part to become a fossil, it must either live within or be moved to a place where it can be buried and isolated from decay*. The more rapid the burial, the less decay and the better the chance of preservation. Burial alone, however, does not guarantee that fossilization will occur, because conditions conducive to decomposition or dissolution often persist to great depths of burial. We have to assume that only a minuscule percentage of organisms become preserved in the sedimentary record.

3.2.2 During the latter part of geologic time, at least, most subaerial environments (those exposed to the open air rather than being underwater) have been fully oxygenated, so the soft tissues of dead organisms, whether plants or animals, are susceptible to decay. Microorganisms like bacteria are especially important in facilitating such decomposition. Many if not most subaqueous (underwater) environments are also oxygenated, owing to the ability of water to dissolve the oxygen of the atmosphere—although the geologic record tells us that that have been times in geologic history when the oceans were largely stagnant, and reducing environments, in which organic matter accumulated in abundance, were widespread.

3.2.3 For organisms to escape decay, burial must be extremely rapid, or the depositional environment must be anoxic (without the presence of oxygen). Some of the best-preserved soft body fossils have been found in deposits that are interpreted to have formed in marine basins in which there is little or no vertical exchange of water, so that the bottom waters are stagnant, but at the same time there is a rain of organic matter from the near-surface waters, the result being anoxic bottom waters. Free-floating organisms that fall to the bottom in such a

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water body have an excellent chance of preservation. Probably the best modern example of such an environment is the Black Sea.

3.2.4 Hard skeletal materials, like bones and shells, have a far high probability of preservation than soft tissues. For a bone or shell to be preserved, it must only survive breakage and abrasion before burial and chemical dissolution of its constituent mineral material before and after deposition. Even if the object is dissolved after deposition, it is likely to be represented by a cavity, which serves the paleontologist almost as well as the entire preserved object. Except in the youngest sedimentary rocks, imprints of the shells of marine invertebrates are just as common as the shells themselves, and usually even more so.

3.3 Fossiliferous Rocks

3.3.1 A rock that contains fossils is said to be *fossiliferous* (in contrast to unfossiliferous—or, perhaps better, nonfossiliferous). Almost all fossils are contained in sedimentary rocks. Not all sedimentary rocks, however, contain fossils. If they parachuted you out of an airplane to land on a random outcrop of sedimentary rock, the chance of your finding a fossil would be rather small— nowhere close to one hundred percent. Fossils are virtually nonexistent in igneous rocks, and they are extremely uncommon in metamorphic rocks, although certain robust body fossils can survive a substantial degree of metamorphism. Finding a fossil in a metamorphic rock is a significant and exciting event for a geologist, because it is extremely difficult otherwise to date the time of deposition of the sedimentary precursors of now-metamorphosed rocks. More germane to this section is that even slight low-grade metamorphism is effective at obliterating, or at least obscuring, the evidence of the small, vulnerable, single-celled organisms that inhabited the early Earth.

3.3.2 Some kinds of sedimentary rocks tend to be more fossiliferous than others. Limestones are the generally the most fossiliferous of sedimentary rocks. That should not be surprising, because most limestones consist in part, or even entirely, of the body parts of shelly marine organisms. Most coarse-grained limestones, and many fine-grained limestones as well, consist mostly of whole shells or fragments of shells. Such fragments, although recognizably derived from whole organisms, are not usually the subject of special study by paleontologists, because they are not sufficiently intact to carry detailed information about the nature of the organisms from which they were derived (although technically they are nevertheless fossils).

3.3.3 In the Precambrian, cherts, together with limestones and shales, are the major repositories of the fossil evidence of early life. You can imagine a tiny, soft-bodied unicellular organism, perhaps no more than several micrometers in size, encased in soft, gelatinous, freshly precipitated amorphous silica from ocean waters. Even if there is recrystallization of the chert, to a microcrystalline

aggregate of quartz crystals, there is a non-vanishing likelihood of at least partial preservation of the organism. The very oldest preserved fossils so far found are of this kind; see a later section.

3.3.4 Many shales, which are derived from freshly deposited mud, are fossiliferous as well, because certain organisms like to live on muddy sea floors. Shales are often rich in trace fossils, but are less so in body fossils except when the chemical conditions during deposition were conducive to preservation rather than decomposition. The best representatives of soft-bodied organisms are from shales, although, frustratingly for paleontologists, instances of such preservation are very uncommon. Many sandstones are fossiliferous as well, although the body fossils in sandstones are usually relatively robust shelly materials, which are not highly susceptible to chemical decomposition. Conglomerates are the least fossiliferous of sedimentary rocks.

4. THE EARLIEST FOSSILS

4.1 Introduction

4.1.1 Before the middle of the twentieth century, the conventional wisdom among geologists (and paleontologists) was that *there were no Precambrian fossils*. I can remember that era well, when I was an undergraduate geology major in the late 1950s. My best friend, a fellow geology major, once confided to me, when we were students, that he would like to be the first geologist to find a Precambrian fossil: what an advance in science that would be! In fact, however, it was during the 1950s that a few geologists and paleontologists began to discover Precambrian fossils. It was the start of a great reorientation in geological thinking.

4.1.2 There were good reasons why Precambrian fossils, now known to be plentiful in the Proterozoic and present, though still scarce, even as early as the early Archean, were virtually unknown. Geological work and thought were dominated by the geoscience "establishment" in Western Europe and the United States, where, basically just by geological accident, there was a major unconformity below the Lower Cambrian, and the rocks beneath the unconformity were mainly crystalline basement rocks—an unlikely venue for fossils. Moreover, no one until the 1950s seemed to have thought to train the advanced microscopic techniques of the time on unmetamorphosed or only mildly metamorphosed Precambrian sedimentary rocks. When they finally did, they found some spectacularly interesting microfossils.

4.1.3 For what it's worth, here's a personal recollection from a now very senior geologist. Once, when I was a undergrad, I went to an evening talk at the Harvard geology department, given by a paleobotanist named Elso Barghoorn. He had been working with a colleague on microscopic examination of a Proterozoic chert unit, in the Canadian Shield, named the Gunflint Formation, an interbedding of chert and volcanics about 2000 Ma old. Together, they discovered a rich fauna

of microfossils, fossilized in the chert. (Apparently, their discovery wasn't just a matter of serendipity: they reasoned that the most likely kind of rock in which to find fossilized Precambrian microfossils would be an unmetamorphosed old chert.) It hit the audience like a bombshell. I remember clearly that one of the audience, the distinguished chairman of the MIT geology department, and a paleontologist himself, stood up at the end of the talk and opined that this was one of the most seminal moments in his professional career, a milestone in the advancement of geological science.

4.2 Archean Fossils

4.2.1 The fossil record of life on Earth is now known to stretch all the way back to the early Archean. In recent decades *there have been many reports of Archean fossils*: by one count, as of 1992, 43 categories of supposed Archean fossils, from 30 sedimentary units, had been reported. Of these, *almost all have at one time or another been questioned as true fossils*. That brings up the question: how does one recognize a given fossil-like object in the sedimentary record as a genuine fossil?

4.2.2 In the case of more recent fossils, during the Phanerozoic, almost all fossils are to some extent at least similar to living descendants. Even when poorly preserved, such fossils are commonly recognized as true fossils. Added to this is the "complexity effect": the more advanced and complex the body morphology of an organism, the more likely is a fossil representative recognized as organic, rather than as some kind of inorganic feature.

4.2.3 Various kinds of objects, with globular, tubular, or other fairly regular shapes, are known to be inorganic, produced by abiotic processes. Examples are mineralized bubble cavities, mineral dendrites (frond-like growths of mineral crystals on fracture surfaces), and non-biogenic aggregates of fossil organic matter. When a geometrically simple fossil-like feature is found in very old Precambrian rocks, particularly when it is not obviously related to some previously authenticated early fossil, there is a natural skepticism about whether it is really biotic rather than the product of some abiotic process. Added to that are problems associated with contamination by modern unicellular organisms during sample preparation.

4.2.3 Scarcity of early Archean fossils is understandable, even if it is assumed that potentially fossilizable life existed at that time. Probably you have already learned, in some previous course, that the early Archean continents were small nuclei, without broad and tectonically stable cratonal areas. There are not many sedimentary successions in which to search for fossils in the first place, and most of them have suffered some degree of metamorphism since deposition.

4.2.4 The most promising targets for the search for Archean fossils have been in the Archean terranes of southern Africa and western Australia. A

particularly promising find was made in the Early Archean Warrawoona Group, in western Australia, in the late 1980s. That part of the Warrawoona Group is dated with confidence at 3540 ± 0.030 Ma. At one particular locality, four taxa of filamentous microfossils were found in a chert layer. The problem is that when the original discoverer and others went back to find the locality, they couldn't find it again! In a situation like this, relocation is important for authentication:

> Clearly, this is a tantalizing set of observations, one suggesting that it must be very probable that cellularly preserved evidence of Early Archean life exists in Warrawoona Group sediments. Just as clearly, however, the available data fall short of providing the critical "hard-nosed" proof that properly should be demanded of discoveries of this sort, discoveries that alter generalizations (in this case, regarding the oldest unequivocal evidence of life on earth) and, thus, become incorporated in college textbooks and even in common parlance. The harsh reality is that because this discovery has not been reconfirmed, the results of this study, despite their presumed validity, are of limited value." (Schopf, 1992, p. 28.)

4.2.5 Never fear. The author of that guardedly skeptical evaluation himself discovered similar fossils in that same Warrawoona Group later (albeit before he wrote the above quotation!). Just to demonstrate relocatability, a person described as a "fledgling graduate student, who had not previously visited the outcrop and was armed solely with maps, notes, and field photographs from the previous ... collecting trip" (Schopf, 1992, p. 29) was able to relocate the locality and collect more material. Below is a brief account of these extremely significant fossils: the oldest undoubted fossils known.

4.2.6 The Warrawoona fossils (Figure 9-4; Schopf, J. W., 1992, Paleobiology of the Archean, in Schopf, J.W., and Klein, C, eds., The Proterozoic Biosphere; A Multidisciplinary Study: Cambridge University Press, 1348 p. Figure 1.5.6, p. 34) are described as filamentous, very dark brown to black kerogenous microfossils (*kerogenous* meaning that they contain kerogen, a general term for decomposition-resistant residual biogenic organic matter in a sedimentary rock). They are composed of well-defined barrel-shaped or discoidal cells, arranged in the form of a long filament, and the terminal cells of the filament are rounded or conical. The lengths of the filaments are some tens of micrometers long, and the individual cells are of the order of a few micrometers in size. These seem to be colonial organisms, with each cell representing an individual unicellular organism. In a few cases there is even evidence of cell division in progress, in the form of partial septa within an unusually long cell. Such microfossils are called trichomes, the general term for chains of filamentous bacteria or algae.

4.2.7 That the fossils are indigenous to the deposit is not an issue here, because the fossils are found within small chert clasts, of sand size, in an enclosing layer of chert. The interpretation is that the chert grains were derived from an even older chert unit and transported mechanically to the site of deposition of the enclosing chert.

4.2.8 What are the phylogenetic affinities of these microfossils? (In plainer English, which known organisms, if any, are they closely related to?) *They are very similar in morphology to Proterozoic and modern cyanobacteria.* One of the big questions about these oldest known organisms is whether they were oxygenic autotrophs or anoxygenic autotrophs. Given that modern cyanobacteria are universally oxygenic photoautotrophs, that's strong but not definitive evidence that these Archean cyanobacteria-like microfossils produced oxygen as well. We'll never know for sure, of course.

4.2.9 One of the uncertainties about early fossils that look much like much younger fossils, or like modern ("extant") organisms is what the specialists whimsically called the "Volkswagen effect": A similar exterior morphology, but, hidden inside, substantial improvements in mechanisms and function.

4.2.10 How about other Archean fossils? Does it seem depressing to you to learn that there are only a few other undoubted examples? Slightly younger microfossils similar to those described above, although not as clearly preserved, are also known from cherts of a unit of chert known as the Onverwacht Group, in southern Africa, dated at 3.540 ± 0.030 Ma, and from younger cherty carbonates (2.768 ± 0.014 Ma) from another unit in western Australia. There are several reported microfossils that are currently considered "dubiofossils" (is that term sufficiently self-explanatory?); some of these are probably also fossils. It seems reasonable to conclude that, as the search for Archean fossils continues, more undoubted cases will be discovered—but probably never more than a handful.

4.2.11 In addition to the Archean fossils described or mentioned above, which are true body fossils, several examples of Archean stromatolites are known. Modern stromatolites are thought to be, at least in part, sedimentary features built by microorganisms, and if that is true of the Archean examples, then that adds to the short list of Archean fossils. The problem is that the fossil nature of ancient stromatolites is inferential. The following section tells much more about stromatolites.

4.3 Stromatolites

4.3.1 Here are three partly conflicting definitions of stromatolites:

"Stromatolites are organogenic, laminated calcareous rock structure, the origin of which is clearly related to microscopic life, which in itself must not be fossilized" (the original definition; Kalkowsky, 1908, translated from the original German)

"Stromatolites are organosedimentary structures produced by sediment trapping, binding, and/or precipitation as a result of growth and metabolic activity of micro-organisms, principally cyanophytes" (Walter, 1976)

"A stromatolite is an attached, laminated, lithified sedimentary growth structure, accretionary away from a point or limited surface of initiation" (Semikhatov et al., 1979)

Make careful note that the first two definitions are genetic and the third is purely descriptive.

4.3.2 Stromatolites are distinctive sedimentary features that are present in rocks as old as Archean. They can be observed forming in subaqueous environments today. Their origin, their significance for paleoenvironmental interpretation, and their significance for the evolution of life through geologic time has been controversial for a hundred years, and continues to be.

4.3.3 The principal features of morphology of stromatolites are easy to describe, in a general way at least. Stromatolites range widely in shape, from domes and cones with rather regular shape, to fairly regular individual cylinders, to irregularly branched columns. The basic motif is that they grew upward from a number of points or small areas to form an array of convex-upward features of positive relief, separated by low areas. Figure 9-5 (Walter, M.R., Grotzinger, J.P., and Schopf, J.W., 1992, Proterozoic stromatolites, in Schopf, J.W., and Klein, C, eds., The Proterozoic Biosphere; A Multidisciplinary Study: Cambridge University Press, 1348 p. (Figure 6.2.1, p. 254)) should give you an idea of the morphological diversity of stromatolites. (Figure 9-5 contains much more morphological information than we can deal with here; it's intended only to give you the "flavor" of stromatolite morphology.) The morphological elements of stromatolites range in size from smaller than a decimeter to many tens of meters. Stromatolites are characteristically *laminated*, typically on a submillimeter to millimeter scale.

4.3.4 The earliest students of stromatolites believed them to be actual organisms, and they gave the various shape categories of stromatolites names in the same way that all organisms, fossil and modern, are given binomial names according to the formal Linnaean naming system. *It is now universally recognized, however, that stromatolites are not individual organisms.*

4.3.5 The great debate about stromatolites centers around *the role of microbial mats in the growth of stromatolites*. The classical view is that stromatolites grow by trapping and binding of fine sediment by a microbial mat at the water–sediment interface. The mat consists of slimy green masses of cyanobacteria or algae, which thrive by photosynthesis in shallow waters. Influxes of fine suspended sediment, carried by waves and currents during episodes of strong water motions, cover the mat. The microbes then grow upward to regenerate the surface of the mat. In the process, after the organic matter of the buried mat is degraded, a lamina of carbonate sediment remains. Such a process can be observed happening today, in just a few places where stromatolites exist.

4.3.6 The problem with this classical interpretation is that *what remains, in ancient stromatolites, is the carbonate sediment*: most or even all of the organic matter that was putatively involved in the growth of the stromatolites has long since been degraded. Moreover, *the texture of the fine carbonate sediment itself has been changed far-reachingly by later diagenesis*. In many cases, microbial fossils are found in association with stromatolites—but that does not, in itself, demonstrate that the stromatolite involved microbial mats: the microbes may just have been non-essential occupants of an abiotically growing stromatolite. It's been estimated that less than one percent of all stromatolites ever described have microfossils associated with them.

4.3.7 Stromatolites are known from as early as the Archean, although their earliest record is scanty (Figure 9-6). They are extremely abundant in the Proterozoic—they are one of the most striking and characteristics aspect of that time in Earth history—although their abundance began to decline around 1000 Ma, slowly at first and then catastrophically around the end of the Proterozoic. The most natural way to explain the decline is the emergence of organisms that either competed with stromatolites for space on the shallow sea floor (seaweeds developed around the same time) or grazed on the microbial mats (gastropods, a.k.a. snails, which emerged near the beginning of the Phanerozoic, or perhaps poorly fossilized soft-bodied earlier metazoans, which emerged near the end of the Proterozoic).

1. Warrawoona Group
2. Onverwacht Group
3. Insuzi Group
4. Uchi Greenstone Belt
5. Yellowknife Supergroup
6. Bulawayan Group
7. Steeprock Group
8. Ventersdorp Supergroup
9. Fortescue Group
10. Hamersley Group
11. Turee Creek Group

0   KILOMETERS   5000
Homolosine Equal Area Projection

Figure by MIT OCW.

Figure 9-6: The distribution of known Archean stromatolite localities

4.3.8 Where does this leave us? I don't know. Just because modern stromatolites involve trapping and binding by microbial mats doesn't automatically mean that ancient stromatolites developed in just the same way, although that's the reigning paradigm. On the other hand, *it's widely believed that most, if not all, ancient stromatolites give evidence of the existence of microbial biota*. Does the clear evolution of the nature of stromatolites reflect evolutionary changes in microbial populations, or gradual changes in such nonbiotic (or only indirectly biotic) things as ocean chemistry? That's still an unresolved question.

4.3.9 Now to get back to Proterozoic microfossils. The record of body fossils of microbes is far more abundant in the Proterozoic than in the Archean.

5. THE FOSSIL RECORD OF PROTEROZOIC PROKARYOTES

5.1 The fossil record of Proterozoic prokaryotes is very abundant, relative to that of the Archean: about three hundred species have been recognized, from a large number of localities. They are found in both shales and cherts. The fossil record of these prokaryotes becomes abundant and widespread by about 2100 Ma. The great majority of these fossil organisms "are of cyanobacterial affinity" (meaning that they look like modern cyanobacteria, in a general way). In particular, a lot of them look like a particular group of modern cyanobacteria called chroococcaleans, which come in ellipsoidal to coccoidal (i.e., spheroidal) shapes, and are both solitary and colonial; others look like a modern group called

nostocaleans, which are colonial in long, filamentous chains. Figure 9-7; Schopf, J.W., 1992, Proterozoic prokaryotes: affinities, geologic distribution, and evolutionary trends, in Schopf, J.W., and Klein, C, eds., The Proterozoic Biosphere; A Multidisciplinary Study: Cambridge University Press, 1348 p. A) Figure 5.4.1, p. 195; B) Figure 5.4.2, p. 196, shows some representative modern cyanobacteria. (No scale was given in the original figures, but I think that these features are of the order of ten micrometers to a few tens of micrometers in size.)

    5.2 Just to calibrate you, slightly, to the nature of these Proterozoic cyanobacteria-like fossils, here are a few comments about modern cyanobacteria. Modern cyanobacteria are unicellular oxygenic photoautotrophs (i.e., they are photosynthesizing plants, with chlorophyll, that produce oxygen during photosynthesis). (Incidentally, cyanobacteria used to be called blue-green algae, but they are not true algae. Algae are eukaryotic plants, only very distantly related to cyanobacteria; see Figure 9-2.)   They resemble bacteria, but they differ in that bacteria are not photosynthesizers. (If you go back to Figure 9-2, you can see that both bacteria and cyanobacteria belong to the domain of Bacteria, so they are relatively closely related.) Most are colonial, forming long filaments. They are extremely widespread in their distribution: they are found in hot springs, soils, freshwater bodies, and the oceans.

    5.3 Not all Proterozoic prokaryotes are cyanobacteria-like. A small minority of them are more like modern bacteria, and some are classed as "problematica" (meaning that paleontologists don't know what to do with them). Whatever their taxonomic affinities, however, it seems clear that *they underwent very little morphological evolution over extremely long periods of geologic time*. It's possible that their internal anatomy and physiology advanced more than their external morphology during that long time (the "Volkswagen effect" mentioned above): there is absolutely no fossil evidence of their innards. Given the relative simplicity of the internal anatomy and physiology of modern cyanobacteria, however, that seems unlikely. This matter has relevance to the important question of whether these Proterozoic prokaryotes engaged in oxygenic photosynthesis. There is, of course, no direct evidence of that, but there is good circumstantial evidence: the atmosphere became oxygenated in the course of the Proterozoic, and if these prokaryotes were the dominant organisms until late in the Proterozoic, it's reasonable to assume that they were photosynthesizers. Or were other organisms, which never became fossilized, responsible for the oxygenation? There's a lesson in all of this: you can see how speculative much of the thought about the Precambrian has to be.

5.4 One of the major geological uses of fossils in the Phanerozoic is time correlation of strata from region to region of the Earth; more on that later, when we deal with the Phanerozoic. (Another of the major geological uses of fossils is in the interpretation of paleoenvironments—an entirely separate matter.) What's clear from the Proterozoic record of prokaryotes is that *they are virtually useless for correlation*.

PART II. NEOPROTEROZOIC LIFE

1. INTRODUCTION

1.1 The Neoproterozoic, from 1000 Ma to the beginning of the Cambrian, at 543 Ma, was indeed an exciting time. It saw the rise of organisms with eukaryotic cells, structurally and metabolically advanced, relative to organisms with prokaryotic cells (which had been around for well over two billion years!). It saw the assembly and then breakup and dispersal of the supercontinent of Rodinia.

1.2 In the course of the Neoproterozoic there were two major intervals of *continental glaciation*. The latter of which was clearly the most extensive glaciation in Earth history. There is good evidence of the existence of extensive glaciers even at low latitudes, and some believe that the Earth at that time was a "frozen ball", described as the *snowball Earth*.

1.3 In conjunction with these changes in climate there were great changes in *geochemical signatures*, most prominently of carbon, leading, for the first time, to the possibility of doing what is called *chemostratigraphy* (making correlations of strata and stratigraphic units from region to region on the basis of their geochemical signatures). Study of the variations in such geochemical signatures through time is, of course, valuable in itself, because of the insight it can provide into the overall Earth environment.

1.4 Near the end of the Proterozoic, there appeared on the scene a fascinating biota of large, well preserved organisms, all of them soft-bodied rather than with biomineralized skeletons, called the *Ediacaran biota*. Were they the precursors of the various phyla of invertebrate animals that exploded near the beginning of the Cambrian, or were they a distinctive and unrelated set of organisms? The matter is not settled.

2. THE RISE OF THE EUKARYOTES

2.1 Eukaryotes and Prokaryotes

2.1.1 The appearance of organisms with eukaryotic cells was a major advance in evolution. Eukaryotic cells are much larger than prokaryotic cells, and they are more advanced in structure and physiology. Perhaps the most striking difference between the two kinds of cells (see background section below for more detail than is included in this paragraph) is that in the eukaryotic cell the genetic material is contained within a cell nucleus, a structure contained within the cytoplasm (the term used for the fluid content of the cell) but isolated from it by its own wall. In prokaryotes, on the other hand, the genetic material is dispersed within the cytoplasm. Moreover, eukaryotic cells contain a variety of special structures and bodies called *organelles*. (The nucleus itself is one such organelle.) The most characteristic of such organelles, besides the nucleus, are *mitochondria*, in which much of the metabolic activity of cell is carried out, and, in the case of plants, *chloroplasts*, in which photosynthesis occurs.

BACKGROUND: PROKARYOTIC AND EUKARYOTIC CELLS

1. There are great differences between prokaryotic and eukaryotic cells. Within each kind, of course, there is considerable variety of structure and biochemistry, but a number of fundamental differences reflect the accepted idea that *eukaryotic cells are a late (in the context of geologic time, that is) evolutionary advance over prokaryotic cells.* don't interpret that to mean that eukaryotic cells are more successful than eukaryotic ells, though: prokaryotic organisms are highly successful in their diverse ecological niches—swarming all over us and within us throughout our lives!

2. Prokaryotic cells are both smaller and simpler than eukaryotic cells. The typical size range of prokaryotic cells is 0.2 to 2 μm (micrometers, or microns) in diameter, whereas eukaryotic cells are much larger, typically 10–100 μm in diameter. All cells, of course, have a cell wall or membrane of some kind, in order to isolate the contents of the cell from the outer world. Cell walls vary greatly in their composition and structure. Prokaryotic cells actually are more complicated than eukaryotic cells. They consist of a chemically complex macromolecular network, and they are semi-rigid.

3. Both kinds of cell are filled with a material called the *cytoplasm*. It is the internal matrix of the cell, in which all of the other internal constituents are embedded. It consists mostly of water but contains proteins, carbohydrates, lipids, inorganic ions, and various low-molecular-weight organic molecules. In eukaryotic cells, in contrast to prokaryotic cells, the cytoplasm is characterized by

a complex internal structure that consists of an assemblage of very small rods and tubules which together constitute what is called the cytoskeleton.

4. The fundamental differences between the two kinds of cells lie most distinctively in internal composition and structure. Eukaryotic cells contain several kinds of specialized structures called organelles. The most characteristic eukaryotic organelle is, of course, the nucleus, which contains the genetic information of the cell. In prokaryotic cells, the genetic material is distributed throughout the cytoplasm rather than being encapsulated in the nucleus.

5. Among several other kinds of eukaryotic organelles, two of the characteristic are mitochondria and chloroplasts. Mitochondria are spherical or rod-shaped bodies distributed throughout the cytoplasm. Much of the metabolic activity of the cell occurs in the mitochondria, including synthesis of ATP (adenosine triphosphate), the compound that powers metabolic processes. Chloroplasts, contained in the photosynthesizing eukaryotes (algae and plants) are membrane-bounded bodies that contain the chlorophyll and the enzymes that are required for photosynthesis. Chloroplasts are able to multiply on their own within the cell, by increasing in size and then dividing into two. (There's a theory, rather generally accepted nowadays, that chloroplasts were once symbiotic photoautotrophic prokaryotes that eventually became an actual internal part of the host cell!)

2.2 How are Eukaryotes Recognized in the Fossil Record?

2.2.1 There has been a longstanding problem—which continues today—about when eukaryotic cells first evolved. The problem is that *the interior content of the cells of organisms are extremely evanescent, and are not preserved in fossils*. How, then, are we to tell whether a given Precambrian unicellular organism was a prokaryote or a eukaryote? One basis is size: *eukaryotic cells are typically much larger than prokaryotic cells*. The problem is that this is not definitive, because there is an overlap in the two size ranges. In the view of most paleontologists, this problem is always going to be with us.

2.2.2 The problem is not quite as hopeless as it seems, however., inasmuch as the details of composition of the cell walls of prokaryotes and eukaryotes is significantly different. The cell membranes of eukaryotes contain a class of compounds called *sterols*, which are complex lipids (a term used in organic chemistry for a wide variety of fats, oils, and waxes) not found in the cell membranes of the prokaryotes. Under the right conditions of preservation (that is, no more than moderate diagenesis, and no metamorphism) the sterols can survive (as what were called *organic fossils* or *biomarkers* in the preceding chapter).

That's taken as excellent evidence that the cells in question are eukaryotic. The problem, however, is that such evidence is regrettably scanty.

2.3 The First Eukaryotes

2.3.1 Remember the business about how molecular biologists can trace the deep evolutionary roots of the present biological world by the techniques of molecular phylogeny—by examining changes in RNA and DNA sequencing that are thought to have been occurring at an approximately constant tempo through geologic time? By this line of investigation, the Eucarya first diverged from the Archaea far back in geologic time. Also, the presence of organic compounds known to be derived from sterols in rocks as old as 2700 Ma place a minimum age on this evolutionary split. (Remember that sterols are characteristic of eukaryotic cells but not of prokaryotic cells.) The generally agreed-upon conclusion from such studies is that *the eukaryotes diverged from the prokayotes very early in geologic history*, as far back as 2700 Ma. The problem is that such a hypothesis (or should we call it a speculation?) cannot be substantiated by the fossil record.

2.3.2 The oldest fossils that can with some confidence be considered eukarotic are the earliest acritarchs (Figure 9-8; Vidal, G., 1994, Early ecosystems: Limitations imposed by the fossil record, in Bengtson, S., ed., Early Life on Earth; Nobel Symposium No. 84: Columbia University Press, 630 p. (Figure 3, p. 307)). Acritarchs are organic-walled microfossils. They consist of a central cavity enclosed by a wall of single or multiple layers of mainly organic composition. They have diameters from a few tens of micrometers to about two hundred micrometers and a generally globular shape, with either smooth walls or spine-like protuberances or more complex surface geometries (which paleontologists describe as ornamentation). Acritarchs consist of a tough, durable cell wall made up of various organic compounds. Paleontologists isolate acritarchs in large numbers from Precambrian shales, by laboratory techniques of hydrofluoric acid digestion of the inorganic part of the rock, leaving just the acritarchs!

2.3.3 The phyletic affinities of acritarchs are not entirely clear. Some resemble the walls of living dinoflagellates, which are unicellular eukaryotic marine plankton, especially abundant in warm seas. Most acritarchs, however, are interpreted to be the remains of special coatings, called cysts, developed by algae (photoautotrophic unicellular eukaryotes) in the resting stage of their life cycle.

2.3.4 Acritarch fossils are common from about 1000 Ma onwards, but they are known as far back as 1800–1900 Ma, from a special locality in China. These earliest acritarchs are similar in general morphology to undoubted later acritarchs, which date back to about 1400 Ma, but there is some residual doubt about whether these fossils might instead be unusually large prokaryotic organisms.

2.4 Evolution of the Eukaryotes

2.4.1 The earliest evolution of the eukaryotes seems to have been very slow. During the course of the Mesoproterozoic (1600 to 1000 Ma), acritarchs became more abundant and more diverse in their morphology. Also during this time, the first uncontroversially eukaryotic organisms made their appearance. Some of these organisms seem to have been multicellular, but there's the common problem of telling apart the truly multicellular organisms from colonial single-celled organisms, without the benefit of seeing the organisms alive.

2.4.2 The earliest eukaryote that can with confidence be assigned to an extant phylum is a red alga from arctic Canada, dated at 1260 to 950 Ma. It's nowadays clear to paleontologists that such fossil records are a clear indication that *complex multicellularity in the eukaryotes developed long before the end of the Proterozoic*.

2.4.3 During the Neoproterozoic, the diversity of eukaryotes, both unicellular (in the form mainly of acritarchs) and multicellular (mainly in the form of algae) became even more abundant. There's a rich record of such organisms from a number of localities around the world. Such a significant evolutionary increase in diversity of organisms is known in paleontology as a radiation.)

2.5 The Ediacaran Biota

2.5.1 A fascinating and still mysterious assemblage of large organisms, called the ***Ediacaran biota***, made their appearance in the latter part of the Proterozoic and survived until almost the end of the Proterozoic (in round numbers, they spanned the time interval from 600 Ma to 550 Ma). They have been known for over fifty years, and finds at widely separated localities around the world continue to be made. These are the first large organisms known. In part, their diverse body plans have some resemblances to certain of the metazoan phyla that made their appearance near the start of the Phanerozoic, but there is continuing controversy over the extent to which these interesting organisms are the precursors of the Phanerozoic invertebrates. As an outsider to the field, the best adjective I can think of to characterize the Ediacarans is *spectacular*.

2.5.2 Back in the 1940s, a survey geologist named Sprigg, working for the geological survey in the Australian state of South Australia, while reconnoitering a mining property found a suite of distinctive fossils in a Neoproterozoic unit called the Pound Quartzite, exposed in an area called the Ediacara Hills. (This is the story as I understand it.) He published a few papers about the biota, but it wasn't until a number of years passed, in the 1950s and 1960s, that the paleontological world at large came to realize the great significance of Spriggs's discovery. The biota he discovered, together with similar biotas in numerous localities of about the same age around the world, have come to be known as the Ediacaran biota. (It has generally been called the Ediacaran *fauna*, but it's not entirely certain that

these were even animals, rather than plantlike organisms—see below— so it's become safer to refer to them by the more general term *biota*.)

BACKGROUND: FAUNA, FLORAS, AND BIOTAS

1. You've probably heard the terms *flora* and *fauna*. The term **fauna** is used to describe *a particular collection of animals that lived in a given place at a given time*. The corresponding term **flora** is used for an assemblage of plants. There are singular nouns; the plural forms are faunas and floras. The more general term, for plants and animals alive, are biota (singular) and biotas (plural).

2.5.3 Ediacaran biotas have been found in the White Sea area of northern Russia, in Ukraine, in the Avalon terrane of southeastern Newfoundland, in England, in Namibia, and in certain other areas. Their distribution thus seems to be worldwide (although keep in mind that the geography then was very different from now). Although dates are not entirely well constrained, the Ediacarans seem to have spanned a time interval from a bit older than 600 Ma to about 550 Ma, a bit before the official beginning of the Cambrian. Their large size and rather diverse and complex body plans suggests, however, that they must have been evolving, in obscurity, for a long time before that. Or did they make a relatively sudden appearance, for evolutionary reasons we cannot know?

2.5.4 A large number of different kinds of organisms are represented in the Ediacaran biota. What they all have in common is that *they are fossils of soft-bodied organisms*: no biomineralization, to produce hard skeletal materials, was involved. As should make good sense to you, soft-bodied organisms are notoriously difficult to preserve—and yet this great variety of organisms managed somehow to be extensively preserved. Moreover, they are preserved not in shales—the diagenetic product of soft muddy bottoms of the kind that have tended to lead to preservation of delicate soft-bodied organisms in more recent geologic times—but in sandstones! They appear as clear imprints on sandstone bedding planes. Some even have an aspect of three-dimensional preservation. It's clear, from the sedimentological evidence of the enclosing deposits, that these organisms lived mostly in shallow ocean waters, where light was available.

2.5.5 They say that a picture is worth a thousand words. Figure 9-9 (McMenamin, M.A.S., 1998, The Garden of Ediacara; Discovering the First Complex Life: Columbia University Press, 295 p. (Figure 2.2, p. 15; Figure 2.8, p. 22; Figure 2.11, p. 25 Figure 2.17, p. 31; Figure 2.18, p. 33; Figure 2.19, p. 35; Figure 2.20, p. 36; Figure 2.22, p. 38; Figure 2.27, p. 41) and figure 9-10

(Seilacher, A., 1994, Early multicellular life: Late Proterozoic fossils and the Cambrian explosion, in Bengtson, S., ed., Early Life on Earth; Nobel Symposium No. 84: Columbia University Press, 630 p. Figure 1, p. 390) show a variety of Ediacaran fossils. Each kind has been named, in the standard binomial Linnaean system of genus and species, although there are long-standing controversies about how to recognize species among the Ediacaran fossils. It's the old problem of lumpers vs. splitters. What is abundantly clear, however, is that there is a wide variety of different kinds of organisms involved.

2.5.6 The variety and complexity of the great many kinds of Ediacaran fossils recognized so far continually astonishes even hardened paleontologists. I can't possibly do justice to that here. Let me just point out one of the most distinctive and mysterious of them: *Dickinsoniana* (represented by four similar species). A picture and a sketch of *Dickinsoniana* are included in Figures 9-9 and 9-10. Here, lifted from the literature, is a basic description, in conventional paleontologic terminology:

> *Dickinsoniana* is oval in shape, broad and flat. It is bilaterally symmetric, with a plane of symmetry bisecting the oval along its long axis. In some specimens there is a raised ridge running along the symmetry line. Both halves of the creature are divided into tubular partitions that run approximately perpendicular to the plane of symmetry at the point where they meet the midline. Moving away from the midline, the tubular partitions become wider and curve gently toward the nearest end of the flat oval body. Adjacent tubular partitions are fused along their lateral edges for almost all of their length. At one end of the oval the tubes are long and constitute approximately one-third of the length of the midline of organisms. At the end opposite to this one, the tubular structures are much shorter. There may be an inward indentation in the perimeter of the oval at this end. The end of the oval with shorter tubules is presumably the end at which new tubular partitions are added during growth. The margins of the oval may show concentric wrinkling. (McMenamin, 1998, p. 33.)

2.5.7 What is the basic nature of the Ediacaran biota? The organisms seem to have been not biomineralized, but yet with much more potential for preservation than the soft-bodied organisms, like jellyfish, with which we are familiar today. In general, they seem to have been large bag-like and sheet-like organisms, with highly diverse body plans but with certain common traits. Most spectacularly, perhaps, is that they apparently were both mouthless and gutless, and without respiratory organs!

2.5.8 If they were so simple anatomically, how did they obtain their food and oxygen? That's a problem that has concerned the experts for a long time, and continues to do so. One idea is that they had such large surface area relative to

their volume that they were able to obtain their oxygen by simple diffusion through their body surfaces, rather than needing to have more complicated oxygen-gathering organs. Their shallow-water environment is consistent with this idea, and the sheetlike form of many of the Ediacaran species is suggestive of this. They could have obtained nutrients by diffusion of free-floating organic compounds in the waters in which they lived, rather than being filter feeders or mouthed scavengers, in the way that later metazoans obtained their food. They seem not to had any complex apparatus for gathering and digestion of food.

2.5.9 One of the ideas about the Ediacaran organisms that has gained some currency in recent years is that they (or at least some of them) had a symbiotic relationship with photoautotrophic microorganisms(single-celled plants), which would have supplied the organism with oxygen. Such a phenomenon has been termed photosymbiosis. But of course we don't really know.

2.5.10 Many, if not most, of the Ediacarans seem to have been *sessile*—that is, living in one place rather than moving around—as opposed to *vagile*. Some might have been firmly attached to the bottom. There is clear evidence that some incorporated sand into their interiors to aid in holding themselves down against currents. The phrase "rock in a sock", describes some of the bag-like but anchored forms quite well! Figure 9-11 shows one prominent paleontologist's concept: the animal had an internal skeleton of cemented sand at the base of its body to help anchor it to the substrate.
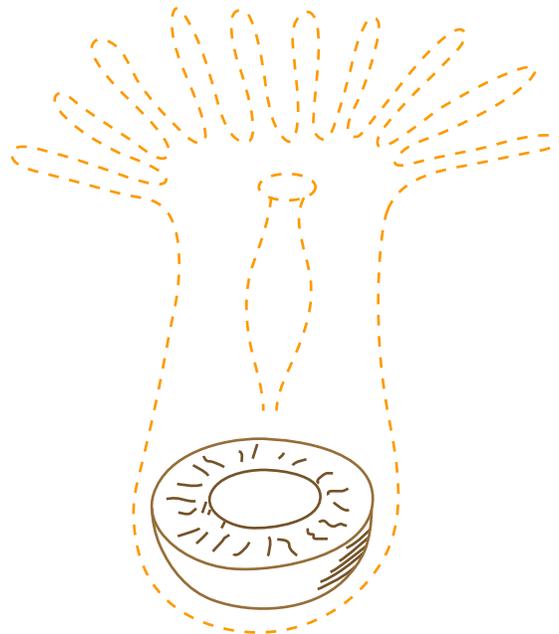
Figure by MIT OCW.

Figure 9-11: Seilacher's concept of an Ediacaran fossil with an internal sand skeleton. The diameter of the sand skeleton is 2 cm

2.5.11 An enduring controversy, not yet settled to general satisfaction, is *whether any of the Ediacaran forms are the predecessors of the later Cambrian invertebrate phyla* that are so well known from the fossil record. Some paleontologists think they can recognize in the Ediacaran biota the precursors of several of the Phanerozoic phyla of metazoan invertebrates. Other paleontologists think that the Ediacaran organisms have no descendants. In the later view, they became extinct without giving rise to the later life forms. There are at least superficial similarities, especially to arthropods (the trilobites, which lived in great profusion on and near the sea floor during much of the Paleozoic, were arthropods), cnidarians (represented today by such beings as sea anemones and jellyfish) echinoderms, and worms, but such similarities by no means prove relationship. One problem in making such connections is that paleontologists have be careful that they not let their so-called "search image" color their interpretations of what might be similar but completely unrelated beings!

2.5.12 There is even a hypothesis out there that the Ediacaran organisms were very large unicellular organisms! There's no way of proving or disproving that, because the cells (cell?) are not preserved. Certain modern animals, called xenophytophores, live on the deep sea floor. They are giant unicellular organisms that form a skeleton of agglutinated sediment particles. Their feeding strategy seems to involve both digestion of organic matter in sediment and direct absorption of nutrients from the seawater. Maybe at least some of the Ediacarans were similarly unicellular.

2.5.13 One prominent student of the Ediacaran biota has proposed that *the Ediacaran organisms lived in a setting without predators*. We are used to the idea that, in the modern world, there are predators and there are prey. That might not have been so at the time of the Ediacaran biota. Perhaps they existed in what has been picturesquely called the "Garden of Ediacara"—a world in which these large and rather advance organisms lived without fear of being eaten! In this view, with the advent of the precursors of the Phanerozoic invertebrates the defenseless Ediacarans slowly became extinct. There is some supporting evidence for this hypothesis. The Ediacarans show little evidence of predator damage, like missing pieces or healed wounds. By Cambrian time, however, such evidence of predation is clear. Maybe the world really did change.

2.5.14 There is little, if any, overlap in the fossil record between the Ediacarans and the later invertebrates that are so characteristic of Cambrian and later times. In terms of trace fossils, however, late in the Ediacaran interval there was a growing abundance of traces, presumably made by non-preservable soft-bodied creeping and burrowing organisms. As time went on, the trace-making organisms seem to have become more and more adept at living and feeding below the water–sediment interface, which is good evidence that they had developed strategies and physiology for much better locomotion on and in the sediment. Maybe these trace-makers were the precursors to the Phanerozoic metazoans we know so well. If so, those poor brainless Ediacaran bags and sheets must have had

no inkling that the small, evanescent trace-makers at their feet (more precisely, their anchoring devices) would eventually spell their doom!

2.5.15 The organisms that constitute the Ediacaran biota lived for some tens of millions of years. By that measure, and in terms of their diverse and complex body plans, together with their worldwide distribution, they can be counted an evolutionary success, even though they eventually became extinct, for whatever reason.

PART III. THE CAMBRIAN EXPLOSION

1. INTRODUCTION

1.1 If you go fossil hunting in Phanerozoic sedimentary rocks, in most places you don't have to go very far to find fossiliferous rocks. If, on the other hand, you try to find fossils in Precambrian rocks, you are almost certain to be doomed to failure. Geologists have known from early on that the obvious fossil record comes in abruptly at the beginning of the Phanerozoic: it's one of those first-order facts of geology. More accurately, however, it's a matter of *the sudden appearance of fossil organisms with hard skeletal materials*; such organisms are said to be biomineralizing. (You've learned already, in a previous section, that there is a significant, albeit not at all obvious, Precambrian fossil record.) This chapter attempts to look more closely at the nature of that change in the fossil record.

1.2 In the previous section you heard about the Ediacaran biotas, which existed for some tens of millions of years near the end of the Neoproterozoic. The relationship between the Ediacaran beings and the later metazoans continues to be controversial. The consensus seems to be that some, or a few (or should I say only a few?) of the Ediacarans are genuinely the ancestors of later metazoans. The appearance of the metazoan phyla we know from the Phanerozoic was a spectacular event in Earth history: it was one of the significant milestones in the history of life, and it happened over an astonishingly short period of geologic time. It's been called the ***Cambrian radiation*** (in the biological context, a radiation is a development of many new life forms by rapid evolution from one or a few precursors during some relatively brief period of geologic time) or the Cambrian explosion. The term "explosion" is, of course, hyperbole (did any other explosion you know of take ten to twenty million years?), but it's seen as appropriate because the event happened in such a short period of time.

2. CLASSIFYING LIVING ORGANISMS

2.1 Since the time of the ancient Greeks, scientists have been trying to classify living beings according to some rational and systematic scheme. The modern system of classification, in which each kind of living being is assigned a genus name and a species name (we are genus *Homo* and species *sapiens*) got its start with Linnaeus (1707–1778; his real, Swedish, name was Karl Linné). Linnaeus spent much of his long life going around and giving things genus and species name—in other words, classifying living things. Eventually the same procedure was adopted for fossils as well.

2.2 There has been a feeling on the part of certain scientists that only fields like physics are "real science", and everything else is "just stamp collecting". In that view, classifying living things is just stamp collecting. In fact, however, classification of living things gets right to the heart of the history of life on Earth. In the field of biology, classifying living things according to an accepted hierarchical scheme is called systematics.

2.3 Up until the middle of the twentieth century, it was generally considered that all living things fell into one or two kingdoms: animals, and plants. Even as far back as the nineteenth century, however, there were biologists who were not comfortable with that neat two-part division, and proposed three-kingdom or four-kingdom divisions, to take account of such things as fungi, yeasts, and bacteria, which don't fit very neatly as either plants or animals. You've seen that nowadays, with the advent of molecular phylogenetics or molecular systematics, mentioned in an earlier chapter, it has become natural to think in terms of three domains: Bacteria, Archaea, and Eukarya.

2.4 An alternative way of classifying all life, past and present, which is based on all aspects of the biology of the beings, and not just molecular phylogenetics, divides all of life into two great domains, the Prokarya and the Eukarya, with the Eukarya in turn divided into five kingdoms: Protoctista (algae, protozoa, slime molds, and certain other kinds of organisms), Animalia (animals without backbones, called invertebrates, and animals, like us, with backbones, called vertebrates), Fungi (mushrooms, molds, and yeasts), and Plantae (mosses, ferns, and other spore-bearing or seed-bearing plants). (In this classification, the domain of the Prokarya contains only one kingdom, the Bacteria, which in turn is divided into two subkingdoms, the Archaea and the Eubacteria).

2.5 These alternative classifications are not the final word: there are other variants out there, and the scene will certainly change, at least in minor ways, as more and more of the details of life are studied, and as the fossil record is uncovered in more and more detail.

2.6 In this section we will be concerned with the Animalia, and in particular, the early development of the Animalia. If the foregoing material on classification of life seems a bit overwhelming to you, here's some more for you

to absorb: how to classify the animals. One way of doing it is to follow the standard taxonomic scheme for all living things. (***Taxonomy*** is *the analysis of the characteristics of a given organism for the purpose of assigning that organism to a taxon*, a ***taxon*** being *a particular group of organisms that are related in some way or to some degree*.) Taxa are arranged according to a hierarchy with several levels, ranging from the broadest and most general (domain, then kingdom) down to the narrowest and most specific (the species, which is usually defined as *a population of organisms that are able to interbreed to produce fertile offspring*—although that definition is less natural for prokaryotes than for eukaryotes).

2.7 Here's the conventional taxonomic hierarchy:

domain
  kingdom
       phylum
          class
              order
                  family
                      genus
                          species

Comments:

• Each of these can be modified by the prefix *super-* or *sub-* to create even more levels in the hierarchy, if the need is felt to arise for a given group of organisms!

• The phylum occupies a somewhat special place in the hierarchy. A ***phylum*** is *a group of organisms whose ancestors became distinctive, by evolution from some even earlier common ancestor, at an early time in Earth history*. There continue to be differences of opinion, on the part of the classifying experts, on which phylum certain organisms belong to, and even about how many phyla there are! Many phyla are represented by only a few kinds of organisms, and some phyla are represented by only extinct species. By one standard classification, there are thirty-seven phyla of animals, only several of which are well represented in the fossil record.

• The only organisms for which we can study physiology as well as anatomy, and, very importantly, reproductive and developmental biology, are living organisms: almost without exception, all we can study about fossil organisms is morphology, and mostly external morphology at that. Traditionally,

the "taxonomic affinities" (that is, how the species should be classified in the taxonomic hierarchy) comes down to educated guesses about evolutionary lineages. For only a surprisingly few fossil species can a clear evolutionary lineage be traced—largely because of the inevitable gaps in the fossil record. In recent years, however, molecular phylogenetics has added enormously to biologists' understanding of the evolutionary history of major groups of organisms.

 • Paleontologists (and neobiologists as well) strive to make their classification of species into higher taxa natural, but the true, right answer is never really at hand; it's a matter of judgment on the part of the practitioners. The only natural basis for recognition of these so-called higher taxa is evolutionary lineages. And how is one to know how evolution actually proceeded? We have no time-lapse movies to tell the tale. This is a fundamental problem not only for paleontologists, who never see their species in the living state, but also for neobiologists, who although they have living species to deal with, are still in the same boat as the paleontologists because they are lacking the dimension of past time.

2.8 There are a few more things you need to hear about before we deal with the early evolution of animals. The kingdom Animalia has been subdivided into two subkingdoms: Subkingdom Parazoa (organisms that lack tissues organized into organs and that mostly have an indeterminate form) and Subkingdom Eumetazoa (true metazoans, with tissues organized into organs and systems of organs). There are also a few kinds of organisms that do not fall naturally into either of these subkingdoms! The Subkingdom Parazoa contains only two phyla: Placazoa (only one genus!) and Porifera (commonly known as sponges, which have been an important component of the world of animals since the initial appearance of animals). Subkingdom Eumetazoa, on the other hand, contains thirty-three phyla.

2.9 The Eumetazoa, in turn, comprise two branches: *radially symmetrical organisms* (the Radiata) and *bilaterally symmetrical organisms* (the Bilateria). Most metazoans (including us!) are bilaterally symmetrical. The Radiata comprise only two phyla: Cnidaria (9400 species, including sea anemones, jellyfish, hydras, and corals), and Ctenophora (comb jellies, a different kind of jellyfish).

2.10 Figure 9-12 (Margulis, L., and Schwartz, K.V., 1998, Five Kingdoms; An Illustrated Guide to the Phyla of Life on Earth, Third Edition: W.H. Freeman, Owl Books, 520 p. (p. 204)) taken from the magnificent book by Margulis and Schwartz on the five kingdoms of life, is the best I've ever found on the nature and phylogenetic relationships of all of the animal phyla. I think it's true (but I'm not entirely certain) that *all of these phyla have a fossil record of some kind*, but what I am sure of is that *the fossil record of most of them is very scanty*—because they are represented entirely by soft-bodied (non-biomineralizing) organisms.

2.11 Almost all of the fossils that are commonly found in Phanerozoic sedimentary rocks belong to the following phyla (in alphabetical order):

Brachiopoda (brachiopods)
Bryozoa (bryozoans)
Echinodermata (crinoids etc.)
Cnidaria (corals)
Mollusca (clams, snails, cephalopods)
Porifera (sponges)
Trilobites (classified either as extinct arthropods or as their own phylum).

3. THE EMERGENCE OF THE METAZOANS

3.1 The Earliest Metazoans

3.1.1 Which are the earliest metazoans depends on how metazoans are defined. Were the Ediacarans metazoans? There's a difference of opinion about that, although the weight of opinion seems to be that, even among the Ediacaran species that seem not to have given rise to Phanerozoic descendants, they were multicellular eukaryotes, and therefore metazoans. There is a minority opinion, though, that the Ediacarans were very large unicellular organisms. Whatever is the case, however, it seems clear that the Ediacaran fossil record disappears well before the rise of the various metazoan phyla, biomineralizing or not, in the Cambrian. (That in itself seems to point toward a fundamental difference between the Ediacarans, on the one hand, and the Phanerozoic metazoans, on the other hand.)

BACKGROUND: THE GEOLOGIC TIME SCALE

1. You should know, from your previous experience in geology, that geologic time has been subdivided into official, named intervals. There is a relative time scale and an absolute time scale. The relative time scale dates back to the 1800s; it was well worked out by the end of the nineteenth century. With the advent of radioisotopic dating techniques, absolute ages in years have been incorporated into the geologic time scale. The absolute time scale continues to be refined, as more and more reliable dates become available. Only recently, for example, the beginning of the Cambrian was revised from 570 Ma to 543 Ma!

(And that had great implications for the timing of the Cambrian explosion; some details later).

2. You need to be exposed to the names of the various subdivisions of Phanerozoic time. There is a hierarchy of geologic time units, order of decreasing scale:

eon   [eonothem]

    era   [erathem]

        period system

           epoch series

              age   stage

(The brackets indicate units that are not in common use.) The reason why there are two sets of terms is that stratigraphers differentiate between time units (also called *chronologic units*), on the one hand, and time-stratigraphic units (also called *chronostratigraphic units*), on the other hand. The time-stratigraphic units consist of the rocks themselves: all the rocks (everywhere in the world!) that were deposited during the given corresponding time interval. You need to understand the difference, for example, between the Cambrian Period (a defined period of time) and the Cambrian System (rocks deposited during the Cambrian Period).

3. Figure 9-13 shows just one part of the official time scale, to introduce you to the terms that are relevant to the Cambrian explosion. The term Vendian is used for the final interval of the Neoproterozoic. The stage and substage names for the Lower Cambrian are taken from Russian localities, where the sections are fairly complete and very well exposed.
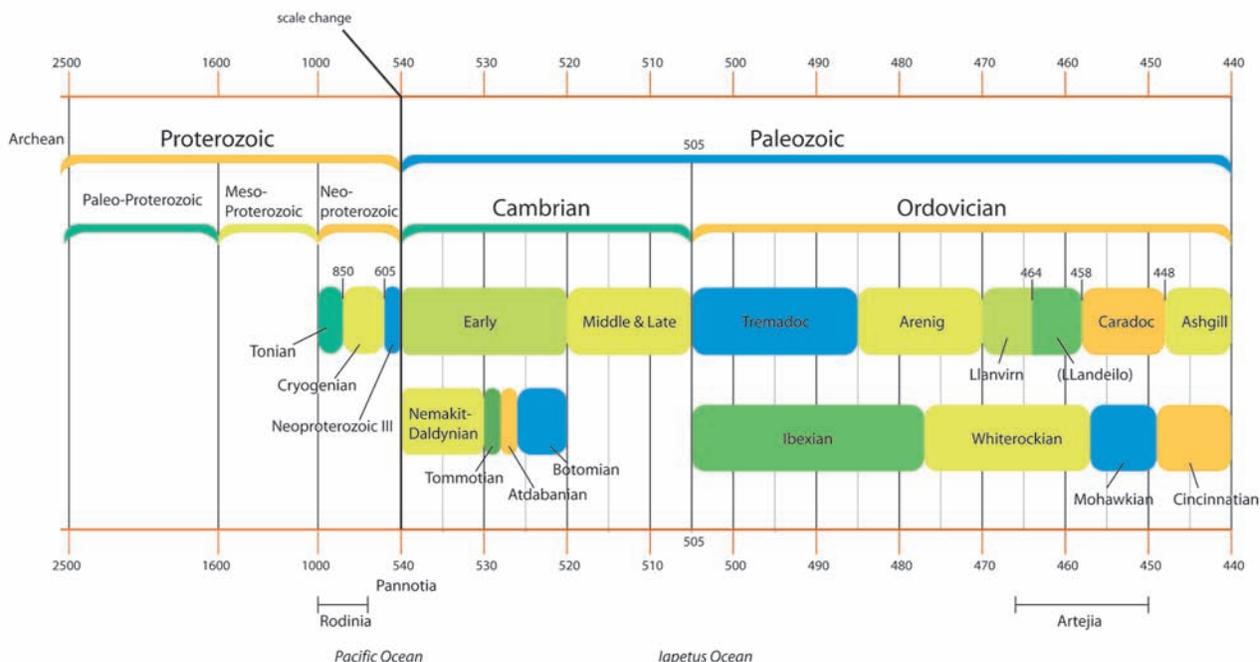
Figure by MIT OCW.

Figure 9-13: The part of the geologic time scale spanning the latest Proterozoic and part of the Cambrian.

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4. What also will be useful for the later material in this chapter is Figure 9-14, which shows the relevant part of geologic time, with stratigraphic terminology as well as key fossils noted.
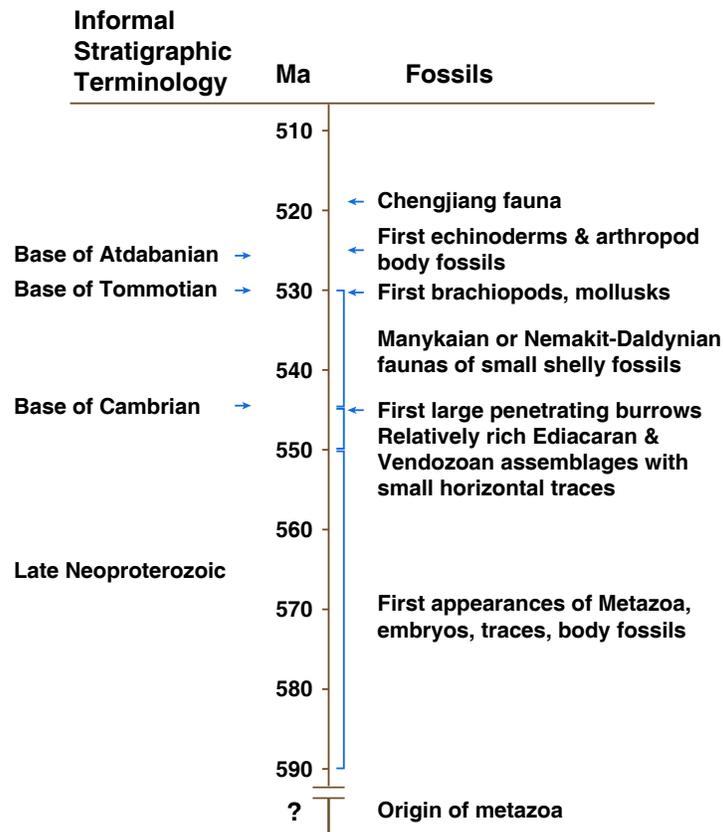
Figure by MIT OCW.

Figure 9-14: Some milestones in the evolution of the metazoa

3.1.2 The fossil record of the metazoans extends back for about forty million years before the Cambrian explosion, which itself spans the age range from about 530 Ma to about 515 Ma (in very round and flexible numbers). The big problem is that that fossil record of metazoans does not contain sequences of fossils that allow tracing the morphological evolution that led eventually to the Cambrian phyla. This long period of obscure and controversial metazoan evolution has been called *the prelude to the Cambrian explosion*.

3.1.3 It was noted in an earlier chapter that, at a certain point in the history of the Ediacarans, trace fossils made their appearance alongside the Ediacarans. At first these traces were very simple: millimeter-wide tracks on the sediment surface. As time went on, the traces become more sophisticated, in the sense that burrowing, in addition to surface tracks, appeared. Presumably, it takes a more advanced soft-bodied organism to burrow through the sediment rather than just creeping across the surface of the sediment. The abundance and complexity of the traces increased up into the earliest Cambrian, even after the disappearance (or almost so) of the fossil record of the Ediacarans. The official base of the Cambrian is now defined on the basis of the appearance of one particularly

characteristic burrowing trace fossil, called *Trepnichnus pedum*, an arcuate horizontal burrow from which branches rise to probe toward the sediment surface.

3.2 The Earliest Biomineralizing Metazoans

3.2.1 The prelude to the Cambrian explosion was not entirely without a fossil record of biomineralizing organisms. A few such fossil species have been discovered in recent years. Here's a brief account of some of them (only genus names are shown):

Cloudina: First found in Namibia and then later at several localities around the world, *Cloudina* coexisted with some of the Ediacarans in latest Neoproterozoic carbonate rocks. It consists of curved, tubular, multilayered shells. The overall appearance is that of a fitted stack of paper or plastic drinking cups.

Namacalathus: Goblet-shaped, with a stem and an upward-flaring cup, a few millimeters to 2.5 cm in diameter, open at the top and with sides perforated with several side holes. The image in Figure 9-15; McMenamin, M.A.S., and Schulte McMenamin, D.L., 1990, The Emergence of Animals; The Cambrian Breakthrough: Columbia University Press, p. 48. B: Grotzinger et al. 2000; was reconstructed by computer from serial sections through a complete fossil specimen.

Namapoikia: A fully biomineralized organism, with a complex and robust skeleton, up to 1 m in width and up to 0.25 m in height. The skeleton consists of multiple continuously connected tubules a few millimeters in diameter. It encrusted perpendicular to the walls of vertical synsedimentary fissure in microbial reefs. It probably represents a cnidarian or a poriferan.

3.3 The Explosion

3.3.1 The term **Cambrian explosion** (less picturesquely, but more accurately, the **Cambrian radiation**) is used for *a brief period of geologic time when many metazoan phyla first appear in the fossil record*. The timing is not entirely pinned down, but it seems clear that the explosion spans the time interval from the middle of the Lower Cambrian, 530 to 520 Ma, and lasting until about 515 Ma. It was during this geologically very brief time period, of the order of ten million years, when organisms with hard and durable skeletal material became common. The recent revision of the time of the beginning of the Cambrian, from 570 Ma to 543 Ma, served to intensify the problem of the Cambrian explosion: it made the permissible time interval much shorter, thus creating an even greater problem for paleobiologists (and, I suppose, providing welcome fuel for the

creationists!). In the context of geologic time, the biomineralizing organisms seem to have exploded into existence. (You saw in an earlier section that there were biomineralizing organisms prior to the great explosion, but they were very few and very uncommon.)

3.3.2 Figure 9-16, which shows the timing of the appearance of phyla in the fossil record, reveals the Cambrian explosion well. As noted earlier, the Cnidaria and the Porifera are generally considered to have made their appearance near the end of the Neoproterozoic, in connection with the Ediacaran biota. Several other animal phyla made their earliest appearance during the period called the Cambrian explosion, almost simultaneously in the context of geologic time. (Many other animal phyla appear in the fossil record much later.) The explosion first manifests itself at the base of the Tommotian Stage, when the earliest biomineralizing brachiopods and molluscs appear in the fossil record. In the succeeding Atdabanian Stage, body fossils of echinoderms and arthropods make their appearance.

Pre Є				Paleozoic					Mesozoic			Ceno
Vendian	**Є**	**O**	**S**	**D**		**C**	**P**	**Tr**	**Jr**	**K**		

- Cnidaria
- Ponfera
- Mollusca
- Brachiopoda
- Ctenophora
- Priapulida
- Onychophora
- Arthropoda
- Phoronida
- Annelida
- Echinodermata
- Chordata
- Hemichordata
- Tardigrada
- Bryozoa
- Nematoda
- Nemertina
- Entoprocta
- Rotifera
- Nematomorpha
- Placozoa
- Mesozoa
- Platyhelminthes
- Gnathostomuilda
- Gastrotricha
- Acanthocephala
- Loricifera
- Kinorhyncha
- Sipuncula

Figure by MIT OCW.

Figure 9-16: The earliest appearance of the various animal phyla in the fossil record

3.3.3 Here's an important point: *the Cambrian explosion involved more than the appearance of biomineralizing animals*. There are a precious and valuable few localities where soft-bodied animals of Atdabanian age are preserved, most notably in Yunnan, in China. That suggests that non-biomineralizing animals underwent an evolutionary radiation as well as the

biomineralizing animals. One could argue that earlier soft-bodied faunas existed but have not been found, or existed but are now obliterated by erosion or metamorphism. But in the explosion interval, along with the expansion in types of body fossils, trace fossils also become larger and more varied, implying that soft-bodied animals participated in the explosion as well.

3.4 *The Burgess Shale*

3.4.1 We can't leave the topic of the Cambrian explosion without considering the fauna of the Burgess Shale. A good case can be made that the Burgess Shale locality is the most famous of all fossil localities. Discovered by the paleontologist Charles D. Walcott near the beginning of the twentieth century (more precisely, on Tuesday, 31 August 1909!) in British Columbia, on the slope of the long ridge between Mount Wapta and Mount Field, a few miles north of the town of Field (and now protected by law from casual visitors), the Burgess Shale locality contains a spectacular assemblage of fossils of soft-bodied organisms, many of them known from nowhere else, along with biomineralized organisms as well. It provides a deeply informative look into the post-explosion world of the Cambrian. Books have been written just about the Burgess Shale fauna.

3.4.2 The Burgess Shale soft-bodied fossils are preserved as flattened imprints along the bedding planes of the shale. Great effort has gone into reconstructing the original three-dimensional bodies on the basis of the imprints. It's an endeavor not without uncertainties, but the results are spectacular. Figure 9-17; A: Whittington, H.B., 1985, The Burgess Shale: Yale University Press. (Fig. 4.7, p. 79.) B: Whittington, H.B., 1985, The Burgess Shale: Yale University Press. (Figure 4.22, p. 87) C: Whittington, H.B., 1985, The Burgess Shale: Yale University Press. (Fig. 4.31) D: Conway Morris, S., 1998, The Crucible of Creation; The Burgess Shale and the Rise of Animals: Oxford University Press, 242 p. (Figure 19, p. 55); just gives you the flavor of these reconstructions. To do justice to them, you need to see photos of the imprints themselves; if you are interested, go to the books by Whittington and by Conway Morris, listed at the end of the chapter.

3.4.3 The great significance of the Burgess Shale fauna is that *it shows how varied the Cambrian animal faunas must have been*. It is universally assumed that the soft-bodied animals represented in the Burgess Shale fauna were ubiquitous in the Cambrian (and presumably later in the Phanerozoic as well) but were only very seldom preserved—under only just the right conditions for preservation. Just imagine how impoverished our knowledge of Cambrian life would have been if the Burgess Shale fauna (and two other similar finds, from somewhat earlier in the Cambrian, and discovered only in recent years—one in Greenland and the other in China) had not been found.

4. WHY THE EXPLOSION?

4.1 There had to have been a reason why the Cambrian explosion happened when it did and how it did. There are two rather different ways of looking at the cause, or causes, of the explosion. In one view, which seems not to be as widely held as the other, it was a consequence of *complex evolutionary interactions among the organisms themselves*, independently of any outside environmental influences. You might think of this as a "biological systems" approach. In the other view, more common, *some aspect or aspects of the late Neoproterozoic and early Cambrian environment caused, or led to, or triggered, the explosion.*

4.2 I'm using the term "environment" here in a very broad sense: such things as climate, ocean chemistry, atmospheric composition, sea level, sedimentation, plate tectonics, continental configuration—and the changes, through time, of all such environmental factors. Also, might there have been just one particular change in one particular thing that triggered the explosion? (That's been termed the "assassin's bullet" hypothesis.) Or must we appeal to a combination of environmental effects, working together in some perhaps very complex way? A variation on the "trigger" metaphor is the "fuse" metaphor: there might have been some event that led to an evolutionary sequence that culminated in the explosion.

4.3 The most widely cited idea about the cause of the appearance of metazoans has to do with *the oxygen content of the atmosphere*. The metazoan phyla that emerged early in the Cambrian must have needed levels of atmospheric oxygen not much lower than at present. If levels were too low before the late Neoproterozoic, then evolution could not have led to the metazoans at that time. There is indeed some independent evidence that the oxygenation of the atmosphere took place in two major steps, one far back in the Proterozoic, in conjunction with the deposition of iron formation, and the other late in the Proterozoic.

4.4 You saw in the preceding chapter that the late Neoproterozoic was a time of spectacular variability in climate (for whatever reason), with snowball-Earth (or at least "icehouse") conditions alternating with much warmer periods. It is natural to think that the synchrony of climate change and metazoan evolution was not fortuitous. Might these severe environmental changes have been the fuse for the rapid evolution of metazoans? It is universally accepted in evolutionary biology that environmental stress tends to result in an increased pace of evolution: populations become small, and they either evolve rapidly to accommodate to the changing environmental conditions or the species they represent becomes extinct.

4.5 Another attractive idea has to do with the occurrence of what might be called the great Cambrian transgression. (Recall that the term transgression, or marine transgression, is used for *a shift of the ocean shoreline in the direction of the land*. Transgression can be worldwide, caused by sea-level rise, or local, caused by subsidence of the lithosphere in the local area. Regressions are the

opposite of transgressions.) One of the first-order facts of the early Phanerozoic is that there was a slow but large worldwide rise in sea level in the course of the Cambrian and into the Ordovician. At the height of the transgression, much of the continent of North America, for example, was covered by shallow seas, thousands of kilometers across and no more than a few hundreds of meters deep. Such seas, called epeiric seas or epicontinental seas, are not well understood, because there are no good examples in today's world of relatively low sea level (more details in the next chapter). The development of such epeiric seas, with their various shallow marine environments, for the first time (in the latter part of geologic time, at least), might have been the trigger for the evolutionary radiation of the metazoans.

PART IV. PHANEROZOIC LIFE

1. INTRODUCTION

1.1 All geoscientists would agree that life on Earth has interacted in fundamental ways with the strictly physicochemical aspects of the planet. You have seen good examples of that idea already in this course: for example, how photosynthesizing organisms have influenced the history of oxygenation of the atmosphere, as well as the broad outlines of climate by way of the role of carbon dioxide in the greenhouse effect. The extreme position in that regard is the *Gaia hypothesis*: that Earth and life have evolved through time in close association with one another, each regulating the other. Most geoscientists seem not to be willing to go quite that far, but it's clear that we can't consider the history of the Earth's physical and chemical environment without taking into account the evolution of life, and vice versa.

1.2 It's not going to be possible to consider, in this section, many of the fascinating twists and turns of the history of life on Earth, which led, in one way or another, to the appearance of the enormous diversity of life forms we observe today. Questions along this line come easily to our minds: How did birds develop flight? Where did the dinosaurs come from, and what was the cause of their demise? What caused primates to become distinct from other mammals? To do justice to such matters, a full course in the history of life on Earth is needed! (I would like to take such a course myself.)

1.3 Here, after some comments on the nature of the fossil record, I'll try to deal with the nature of evolution itself, to give you the flavor of how paleobiologists view the history of life, and then deal specifically with the history of what are called mass extinctions: specific, and catastrophic, times in Earth history when, for whatever reason or reasons (and the nature of those reasons is controversial) large percentages of all living species became extinct, opening the way for explosive radiations of new life forms to fill the vacated niches. In the

process, we'll look at the nature of asteroid impacts, which are implicated in at least some of the mass extinctions.

2. THE NATURE OF THE FOSSIL RECORD

2.1 Generations of paleontologists have agonized over the incompleteness of the fossil record. Some even admit to a kind of inferiority complex, arising from the necessity of having to lead their professional lives working on what they perceive to be an inadequate database. Here's a telling quotation along these lines:

> Paleontologists often give the impression that they don't believe in their own subject and the data that fossils provide. Indeed, paleontology suffers from several misperceptions which, because they are often propounded by paleontologists themselves, make us our own worst enemies. (S.K. Donovan and C.R.C. Paul, 1998, p. 1.)

2.2 That the fossil record is incomplete is beyond any doubt: we can't possibly have a census of all of the organisms that have ever lived. That's not what worries paleontologists, though: what's troublesome is that it's thought that *we are not even close to having a census of all of the species that have ever existed*. (Neobiologists generally agree that we're not even close to having a complete census of existing species!)

2.3 The record of marine biomineralizing species is generally thought to be fairly good; the problem lies more with species of soft-bodied organisms, and with species of organisms that lived on land, where environments conducive to preservation are much less common than in the ocean. Another way of putting this is that *the fossil record is strongly biased in favor of skeletalized species*.

2.4 Various attempts have been made over the years to assess the degree of completeness of the fossil record. Many methods have been proposed. Here are some general considerations, which may not be wildly wrong. Two of the approaches that have been taken, presumably complementary, are as follows. First, ,we know that something like ten percent of all extant species are skeletalized and therefore highly likely to be represented in the fossil record. If we assume that the proportions of skeletalized and nonskeletalized species have been about the same through Phanerozoic time, then, given that almost none of the nonskeletalized species have been preserved, *the fossil record is about ten percent complete*. Second, in the Burgess Shale fauna, again something like ten percent (in very round numbers) of the species represented are skeletalized. If the Burgess Shale fauna is at all typical of later times in the Phanerozoic, in terms of the proportions of skeletalized vs. nonskeletalized forms, then, again, the fossil record is about ten percent complete. The number "ten" here is of course extremely elastic—but the foregoing line of reasoning suggests that the true figure is much

greater than just, say, one percent, but much less than, say, half. Maybe that gives us the flavor of the matter.

2.5 Paleontologists make a distinction between the *completeness* of the fossil record and the *adequacy* of the fossil record. Those two concepts are related but different: the record can be incomplete but still adequate for the pursuit of paleontological problems, as well as for addressing broader questions in geology and biology.

2.6 Here's just one example of how the incompleteness of the fossil record has affected the thinking of paleontologists about the adequacy of the record. Do species evolve along gradual trends, or do they develop abruptly (in the context of geologic time, that is) after long periods of stasis? The fossil record is almost always so full of "holes" that the matter can seldom be decided on the basis of the fossil record. The number of examples of gradual evolutionary trends is amazingly small; according to one authority, they can be counted on the fingers of two hands. Paleontologists have seemed to assume, tacitly, that gradual trends are the norm but just can't be identified owing to the inadequacy of the record. But maybe such trends are the exception rather than the rule.

3. EVOLUTION AND SPECIATION

3.1 The term species has appeared often so far in this chapter, without being defined. What is a species? The species is the fundamental taxonomic unit, in both paleobiology and neobiology. Roughly speaking, a species is one particular kind of organism. More technically, a species could be defined *as a population of organisms capable of fertile interbreeding*. The concept of species is thus natural, not arbitrary.

3.2 Of course, there is some degree of variability, in morphology and physiology, from organism to organism within a species. Variation of this kind is the stuff of natural selection—the process by which species change by preferential survival of organisms with certain features within a species.

3.3 All "non-creationists", scientists and nonscientists alike, are convinced that the living world has developed by a process of evolution. Almost all scientists accept that as fact. What has been controversial, and about which debate continues, is *the nature of the processes by which evolution takes place*—although by now, since the time of the neo-Darwinian "second revolution" in the mid-twentieth century, there has been general agreement about the broad aspects of evolution. Incidentally, there were evolutionists around before Darwin: they just didn't have the right ideas. It was Darwin, with his theory of evolution by natural selection, that put the study of evolution on its modern footing.

3.4 Darwin described his theory as evolution by natural selection. The basic idea is that the members of any species of animals are not identical: they vary in

their characteristics, in numerous ways, as a reflection of their genetic material. Darwin knew this well, in part because of his close familiarity with animal breeding. It was actually a rather revolutionary concept in science: before his time, it was generally assumed that the members of a species were all identical.

3.5 Variation is the essential prerequisite for evolution. All house sparrows look just about alike to us (if we look at all that are the same sex and the same age), but if we were to measure things like beak shape we would find small but significant differences. Such variation among the members of a species means that they differ, if only slightly, from individual to individual in their success in survival and reproduction. The overall characteristics of the species tends to drift with time, in light of this differential success in reproduction.

3.6 The origin of the variation is mutation, the process by which genes are altered, occasionally, as the DNA of the individual replicates itself. Think of these mutations as just "mistakes of copying". Most mutations are deleterious to survival, but now and then a beneficial mutation arises, which offers the organism a greater chance of survival and reproductive success. As such a beneficial mutation spreads through the population, the species has undergone change. Of course, Darwin knew nothing about genetics, let alone nucleic acids and DNA— but he realized the significance of mutations for evolution by natural selection.

3.7 Evolution of a species by natural selection is especially rapid when the population is small and environmental conditions are changing rapidly. Under those conditions, only the very fittest individuals survive to reproduce, and any variations that have adaptive value are strongly selected and then can spread rapidly through the small breeding population. If environmental stresses are so great that the evolutionary response of the population of the species can't keep up, however, the species becomes extinct.

3.8 If you would like to read a spectacular account of a long-term study of evolution by natural selection in action, I recommend *The Beak of the Finch*, a recent book about a decades-long research program on the finches of a very small island in the Galápagos, by Weiner; see the reading list at the end of the chapter.

3.9 The *development of new species from old species* is called **speciation**. The nature and processes of speciation have been the topic of heated debate among neobiologists and paleobiologists alike. In a somewhat oversimplified view, there are two ways new species can evolve. The older species can change gradually (or not so gradually) into a new species, as implied in the preceding paragraph. If the change is gradual, it might be very difficult to draw the line between the two species, even though the accumulated changes necessitate the recognition of two distinct species. (There's the hidden problem here, which arises from the accepted definition of a species as a population of organisms that can interbreed to produce fertile offspring: if the populations in question are widely separated in time, there's no way of testing the new population against the definition!)

3.10 Drawing the line between the two species is not as difficult in practice as it might seem, however, because of the spottiness of the fossil record. The changes in species have usually been fast enough that the holes in the record prevent identification of the intermediate forms. This gets us back to the statement earlier in this section that documented instances of trends of gradual evolution are rare.

3.11 There's another route of speciation, having to do with geographic (or, more generally, environmental) isolation. The populations of given species ordinarily occupy some rather large geographic range. To the extent that the individuals of the population do not roam very far from their places of birth (or, more precisely, the range of mobility of the individual is much smaller than the overall range of the species), then there is the possibility that parts of the overall population that are located in different geographic areas might evolve along different paths. In such a way, a single species might evolve into two contemporary species by geographic isolation. This is especially likely when a small part of a population becomes isolated from the rest of the population by some new environmental barrier (for example, a change in climate or in sea level).

3.12 Here is a final, but significant, note. It is good to keep in mind that paleontologists have no way of verifying that a given species they choose to "erect" was really a species! What paleontologists do in practice is to collect a small or large number of individual specimens which are closely similar among themselves in morphology but which are different in morphology from other related organisms, and then assume that that group of fossils represents what was once a species in the neobiological sense of being an interbreeding population. They are probably right, usually, but clearly there is no way of ever knowing.

4. CLADISTICS

4.1 You heard in an earlier section about taxa, taxonomy, and systematics. Taxonomists place species into genera, and genera into families, etc., in accordance with their best guesses about the evolutionary history of the species. *Taxonomic classification changes as understanding of the evolutionary picture grows.* Sometimes, for example, a species is removed from one genus and put into another. It's not that the species has changed—it's just that the understanding of the evolutionary history of that species has changed.

4.2 There's another, and less formal, way of classifying groups of organisms, which is different from the formal taxonomy of species, genera, etc., but complementary to it. It's called ***cladistics***. Cladistics is an attempt to trace phylogeny—the evolutionary pathways by which given species appeared. In cladistics, species are organized into what are called clades. A ***clade*** is *a group of species that all descended from a common ancestor.*

4.3 For an analogy to cladistics, think in terms of a branching tree. Such a tree has a single trunk, which branches into a number of main limbs. Each limb then branches into smaller limbs, and so on, until the tips of the twigs are reached. The trunk of the tree represents the common ancestor of all of the species represented by all of the terminal twigs. Two twigs that branch from the same larger twig represent a clade (a clade with only two species in it), because they have the same common ancestor. Every clade began with a single branching event that produced the ancestor species of the clade. (The only exception to that last statement is the clade that consists of all the species through all of geologic time, on the assumption that they all had one common ancestor.)

4.4 The idea behind cladistics is to try to recognize groups of species that share a set of characters that evolved as new features in a common ancestor and then passed to all of the descendant species. The evolutionary state that existed before those new characters evolved is called the primitive state, and the evolutionary state that exited after the new characters evolved is called the derived state. Here's an example, to make that real to you. All living mammals have fur, but no other living organisms do. The natural assumption is that fur was inherited from a common ancestor of all living mammals. That makes mammals a clade. That hypothesis is strengthened by the observations that all living mammals are warm-blooded and all of them suckle their young.

4.5 Diagrams that express the paleontologist's concept of a clade (that is, the phylogenetic history of all the species of the clade) is called a ***cladogram***. Figure 9-18 shows an example of a cladogram that shows the evolutionary history of three species that constitute a clade. Cladograms always show the species of the clade along the upper edge of the diagram. There are three possible evolutionary lineages that could account for the three species of the clade. In each of the versions, the development of the novel feature that separates the primitive state from the derived state is at a qualitatively different point in the arrangement. In the upper diagram, species B and C form a smaller clade in themselves; in the middle diagram, species A and B form the smaller clade, and in the lower diagram, species A and C form the smaller clade. How would it be known which is the appropriate version? By study of the sharing of derived characters.
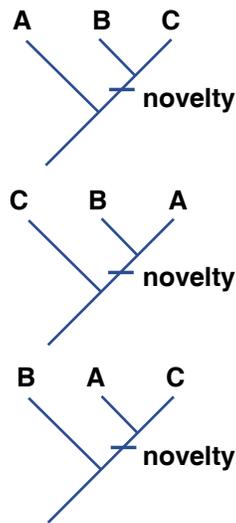
Figure 9-18: Three possible cladograms (expressing three different hypotheses) for the evolutionary relationships of three species that constitute a clade

4.6 To make things more real to you, Figure 9-19 is a cladogram that deals with five major classes of animals (formally recognized classes—as taxa, that is). In this hypothesis (and that's what it represents, a hypothesis, subject to modification if necessary), fishes are the ancestors not just of living fishes but also of living amphibians, reptiles, birds, and mammals. Note the particular topology of the cladogram: tetrapods evolved from fishes by the acquisition of a particular derived character (four legs), then reptiles and amphibians developed from a common tetrapod ancestor, and so on.

4.7 The cladistic approach leads to some startling insights. For example, you can see from the cladogram in Figure 9-19 that humans are derived fishes, derived amphibians, and derived reptiles, all at the same time. Even more startlingly, the case can be made that humans are, in a real sense, derived cyanobacteria! Here's a little poem that expresses the idea:

The human species has thrived
In the short time since we arrived
But the cladist affirms
That we are only worms
Even though we are somewhat derived.

(Richard Cowen, 2000, History of Life, Third Edition, p. 50.)

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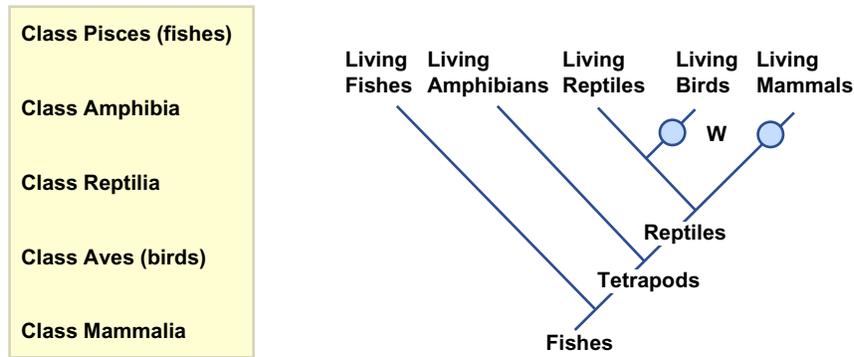
Figure 9-19: (Left) The conventional taxonomic classification of the vertebrates. (Right) a cladogram for the invertebrates

5. IMPACTS OF EXTRATERRESTRIAL OBJECTS WITH THE EARTH

5.1 This section deals with the nature of impact events, what's known about their frequency through geologic time, and the implications for the history of life on Earth. Meteorites are at the small end of the range of extraterrestrial bodies that make impact with the Earth. Over the history of the Earth, such extraterrestrial bodies have ranged in size all the way up to the infamous Mars-size impactor that is now thought to have resulted in the formation of the Moon. That was a uniquely large event, but impacts by bodies hundreds of kilometers in diameter are known during later geologic history, even into the Phanerozoic.

5.2 What happens when a large, fast-moving impactor strikes the surface of a rocky planet like the Earth? There's an important distinction based on the closing speed of the impactor. If the closing speed is greater than the speed of sound (that is, the speed of compressive elastic waves, of the kind that are generated by earthquakes), then strong shock waves are set up (analogous to the sonic boom you hear from an airplane traveling at greater than the speed of sound in air), which destroy both the impactor and the target material. Such impacts are said to be supersonic. They are the most destructive.

5.3 Think in terms of the energy carried by the impactor, versus the energy required to do damage to the impactee. Here's some material, slightly paraphrased, from Lewis (1997, p. 397), for a hundred-meter asteroid hitting the surface at 20 km/s. (Note: an erg is the cgs unit of work and energy. It's equal, to one dyne-centimeter. To make that more familiar, we can convert it to foot-pounds: one dyne-centimeter is equal to about 7.5×10^{-8} foot-pounds. A foot-pound is the work you do when you lift a one-pound weight upward for a vertical distance of one foot. According to my back-of-the-envelope computations, a dyne-centimeter is about the work you would do if you jack up a twenty-five-cent piece by a few thousandths of an inch!)

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The kinetic energy density [the kinetic energy per unit mass] of the impactor is 2×10^{12} erg/g. The energy required to crush a typical rock is a little above 10^8 erg/g. To heat it to its melting point requires about 10^{10} erg/g, and to vaporize it requires less than 10^{11} erg/g. Thus the impactor carries enough kinetic energy not only to vaporize itself completely, but also to crush up to roughly 10^4 times its own mass of target rock, melt roughly one hundred times its own mass, or vaporize about ten times its own mass. Alternatively, it carries enough kinetic energy to accelerate a hundred times its own mass to a speed of 0.1 times its impact speed. In reality, an impact does all of these things to some degree and divides its energy over all these possible outcomes. Thus an impactor may crush one thousand times its own mass of rock, melt ten times it mass, vaporize a few times its own mass, and eject one hundred times its mass at speeds of tens to hundreds of meters per second and still give off a substantial amount of energy as seismic waves and radiation from the fireball.

5.4 Figure 9-20; Lewis, J.S., 1997, Physics and Chemistry of the Solar System: Academic Press, 591 p. (Figure IX.15, p. 398); shows the progression of a typical supersonic cratering event. Here, again paraphrased from Lewis (1997), is a description of the events shown:

The impactor is crushed and flattened by the enormous transient pressures caused by its deceleration, pushing a cavity into the target. The region of the target closest to the projectile is heated so strongly that, as the peak shock is unloaded by the expansion of the debris from the explosion, it vaporizes. A much larger volume, usually with several times the radius of the vaporized zone, is thoroughly crushed and partially melted. Since the effective center of the explosion is well below the surface of the target, the explosion blasts out a substantial mass of rim material in a cone above the explosion site.

5.5 The environmental consequences of a major impact are not fully understood. (Humankind has never experienced one—yet!) Enormous quantities of mineral dust would be injected into the atmosphere, all the way up into the stratosphere, from which it would take months to years to clear by settling. During that time, sunlight reaching the Earth's surface would be reduced to only a small percentage of normal. To the extent that either the impactor or the target area contain sulfur-bearing materials, there would be a high concentration of sulfur dioxide particles in the atmosphere, causing acid rain far more intense than what we now experience from burning of fossil fuels. The heat from the fireball, which itself might last only minutes, might be sufficient to set wildfires of even subcontinental or greater size, putting more smoke and dust into the atmosphere. An impact in the ocean would generate seismic sea waves of gigantic proportions.

Such effects have serious albeit uncertain consequences for the survival of life on Earth.

5.6 What is the nature of the bodies that have made impact with the Earth? It's common to hear that they are asteroids, which, remember, are rocky bodies with "ordinary" orbits (that is, nearly circular, and in the general plane of the solar system), but it's now believed that *most of the larger ones are comets*, which have highly irregular orbits and range in distance from the Sun to far beyond the limits of what we think of as the solar system. It's common to hear that comets are big iceballs, but keep in mind that they have rocky cores, and it's those rocky cores that would do the damage upon impact. Another thing about comets is that, because of their less regular orbits, their closing speeds can be much greater than the typical closing speeds of asteroids.

5.7 What do we know about the record of impacts? There was a period, very early in Earth history but after the Earth had become largely accreted, called the late heavy bombardment. For long after that, however, and into recent geologic time, there has been a continuing albeit occasional bombardment of objects both large and small. There are some who think they detect an actual increase in frequency of impacts in latest geologic time, in the most recent hundred million years or so, but that is a controversial idea.

5.8 The number of well-documented large impacts is increasing steadily, as geologic work on all of the continents continues. In recent years, especially after the advent of the theory of a really big impact that marked the Cretaceous–Tertiary boundary, the discovery of impact structures has accelerated. The known record is getting better and better, but there will always be the problem that the processes of weathering, erosion, and sediment deposition on the active surface of the earth tend to blur and finally obliterate the record of impacts, thus biasing the record in two ways: minimizing the frequency of earlier impacts, and skewing the record of early impacts toward the larger events (which are less susceptible to obliteration).

5.9 Figure 9-21 gives you some data on known large impacts through geologic time. Part A gives data on impact structures in North America, and part B gives data for the entire world. There have been some really big ones.

A. Large craters on the North American Craton, listed in order of increasing age; these data have been taken from Hodge(1994)

Name	Latitude (degrees)	Longitude (degrees)	Diameter (km)	Age (Ma)
Sythemenkat Lake	66	151	12	0.01
Haughton	75	90	20.5	21
Mistastin Lake	56	63	28	38
Montagnais	43	64	45	52
Marquez Dome	31	96	15	58
Manson	44	95	35	74
Eagle Butte	50	111	19	< 65
Steen River	60	118	25	95
Carswell	58	110	39	115
Sierra Madera	31	103	13	> 100
Wells Creek	36	88	14	200
Manicouagan	51	69	100	212
Saint Martin	52	99	40	220
Clearwater Lake West	56	74	32	290
Clearwater Lake East	56	74	30	290
Charlevoix	48	70	54	357
Kentland	41	87	13	> 300
Slate Island	49	87	30	> 350
Beaverhead	45	113	15	600
Nicholson Lake	63	103	12.5	> 400
Presquile	50	75	12	> 500
Sudbury	47	81	200	1850

B. Basic characteristics of impact structures mentioned in the text

Crater name	Location	Latitude	Longitude	Age (Ma)	Diameter (km)
Acraman	Australia	S32°1'	E135°27'	>450	90
Barringer	USA	N35°2'	W111°1'	0.049 ±0.003	1.186
Beaverhead	USA	N44°36'	W113°0'	0.600	75
Boltysh	Ukraine	N48°45'	E32°10'	88 ± 3	24
Bosumtwi	Ghana	N6°30'	W1°25'	1.03 ± 0.02	10.5
Brent	Canada	N46°5'	W78°29'	450 ± 30	3.8
Chesapeake Bay	USA	N37°17'	W76°1'	35.5 ± 0.6	85
Chicxulub	Mexico	N21°20'	W89°30'	64.98 ± 0.05	170
Dellen	Sweden	N61°48'	E16°48'	89.0 ± 2.7	19
Eagle Butte	Canada	N49°42'	W110°30'	<65	10
East Clearwater	Canada	N56°5'	W74°7'	290 ± 20	26
Gardnos	Norway	N60°39'	E9°0'	500 ±10	5
Gosses Bluff	Australia	S23°49'	E132°19'	142.5 ± 0.5	22
Goyder	Australia	S13°29'	E135°2'	>65	7
Haughton	Canada	N75°22'	W89°41'	23 ± 1	24
Janisjarvi	Russia	N61°58'	E30°55'	698 ± 22	14
Kelly West	Australia	S19°56'	E133°57'	>550	10
Manicouagan	Canada	N51°23'	W68°42'	214 ± 1	100
Mistastin	Canada	N55°53'	W63°18'	38 ± 4	28
Mjoinir	Norway	N73°48'	E29°40'	143 ±20	40
Montagnais	Canada	N42°53'	W64°13'	50.5 ±1 5	45
Morokweng	South Africa	S26°28'	E23°32'	145 ± 0.8	70
Popigai	Russia	N71°40'	E111°40'	35.7 ± 0.2	100
Ries	Germany	N48°53'	E10°37'	15 ±1	24
Slate Islands	Canada	N48°40'	W87°0'	<350	30
Soderfjarden	Finland	N62°54'	E21°42'	0.600	5.5
Sudbury	Canada	N46°36'	W81°11'	1850 ± 3	250
Tookoonooka	Australia	S27°7'	E142°50'	128 ± 5	55
Vredefort	South Africa	S27°0'	E27°30'	2023 ± 4	300
West Clearwater	Canada	N56°13'	W74°30'	290 ±20	36
Zhamanshin	Kazakhstan	N48°20'	E60°58'	0.9 ±0.1	13.5

Figure 9-21: Data on known large impacts through geologic time

Figure by MIT OCW.

Finally, Figure 9-22 is a graph of impact frequency against impact energy. The upper line gives the equivalent information for earthquakes. Any event larger than about the zone delineated by the vertical dashed lines would have severe global consequences.
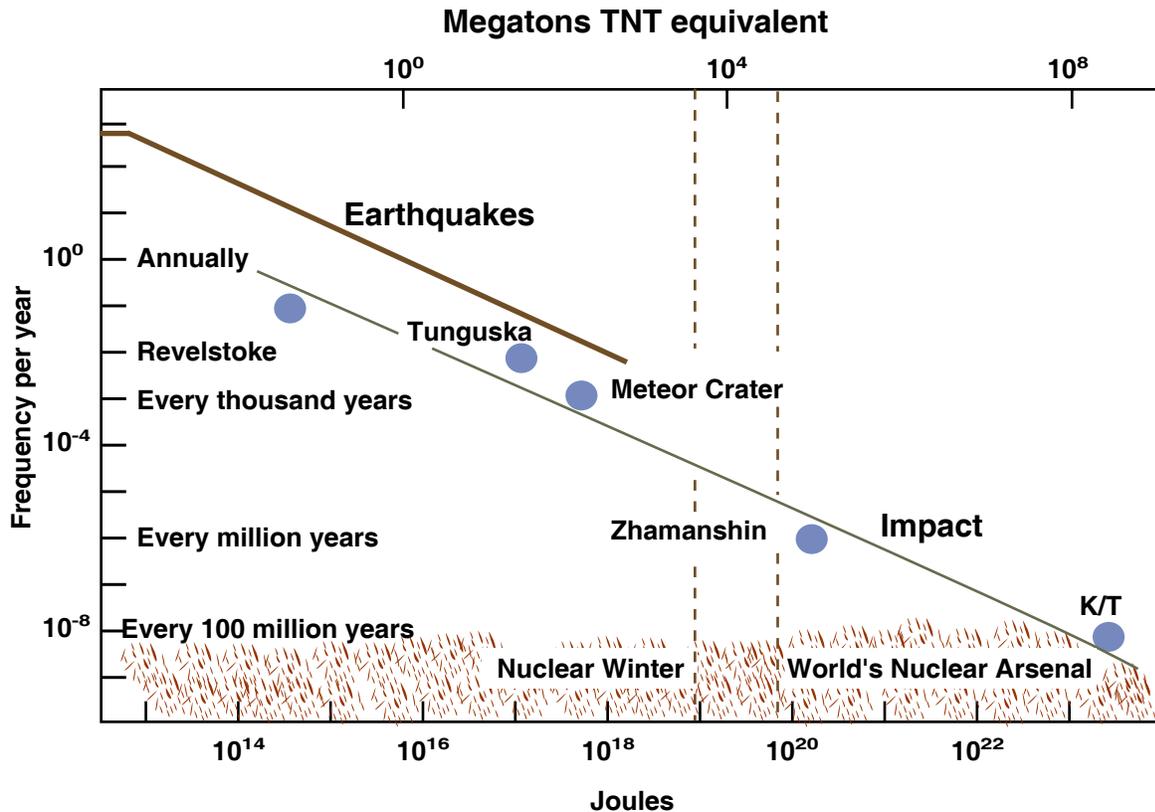
Figure by MIT OCW.

Figure 9-22: Graph of impact frequency vs. impact energy

5.10 Even small events would have serious regional consequences, depending of course on location. The Tunguska event, which occurred on 30 June 1908 (it was an explosion of an extraterrestrial body, of size less than a hundred meters, in the atmosphere, before the body had a chance to make impact with the surface), flattened trees over an area of two thousand square kilometers in Siberia. Can you imagine the devastation that would have ensued if that event had happened over the eastern U.S., western Europe, or heavily populated areas in India or China? From the graph, you can see that the frequency of such an event per year is about 10^{-2}, meaning that the average recurrence interval is only of the order of a hundred years. We shouldn't be holding our breath, but the likelihood of another event of that kind within the lifetimes of some of you in the class is quite high.

6. MASS EXTINCTIONS

6.1 The evolution of life on Earth has been fraught with setbacks. At various times in the geologic past, unusually large numbers of species have become extinct over short periods of geologic time. Such events have been termed mass extinctions. Because skeletalized marine invertebrates have a record that's far better than that of soft-bodied marine organisms, or of terrestrial organisms in general, the nature of mass extinctions has been based largely on them.

6.2 There is no doubt that mass extinctions have occurred. The greatest mass extinction of all time (no, it's not the one at the end of the Cretaceous, which is alleged to have involved the demise of the dinosaurs) was at the end of the Permian: *more than ninety percent of all extant species became extinct!* The controversy has revolved around the cause (or causes) of the extinctions.

6.3 Mainly, three possible causes have been invoked for mass extinctions:

- impacts of large extraterrestrial bodies
- outpourings of continental flood basalts
- sea-level falls leading to major regressions

It seems to make sense that large impacts might lead to widespread, catastrophic extinction, given the effects that such impacts are thought to have on the Earth surface environment. The other two possible causes have been much less publicized, but they have their responsible proponents.

6.4 At certain times in Earth history, there have been enormous outpourings of basaltic lava onto the Earth's surface. The basalts thus formed, which cover large areas to great thicknesses, are called ***flood basalts***, and the regions affected are called ***large igneous provinces***. They form great volcanic plateaus, both on land and under the ocean. Figure 9-23 shows the locations of major continental flood basalts and submarine basalt plateaus. These massive emplacements of volcanic rocks originate by processes seemingly unrelated to the normal basaltic volcanism associated with sea-floor spreading. They are generally thought to be associated instead with large mantle plumes. Humankind has never experienced a such a period of outpouring of basaltic magmas: the rates must have been orders of magnitude greater than during any volcanic eruptions in human history. Such volcanism must have injected enormous quantities of greenhouse gases and particulates into the atmosphere and oceans, and the climatic effects, especially arising from the continental outpourings, must have been substantial.
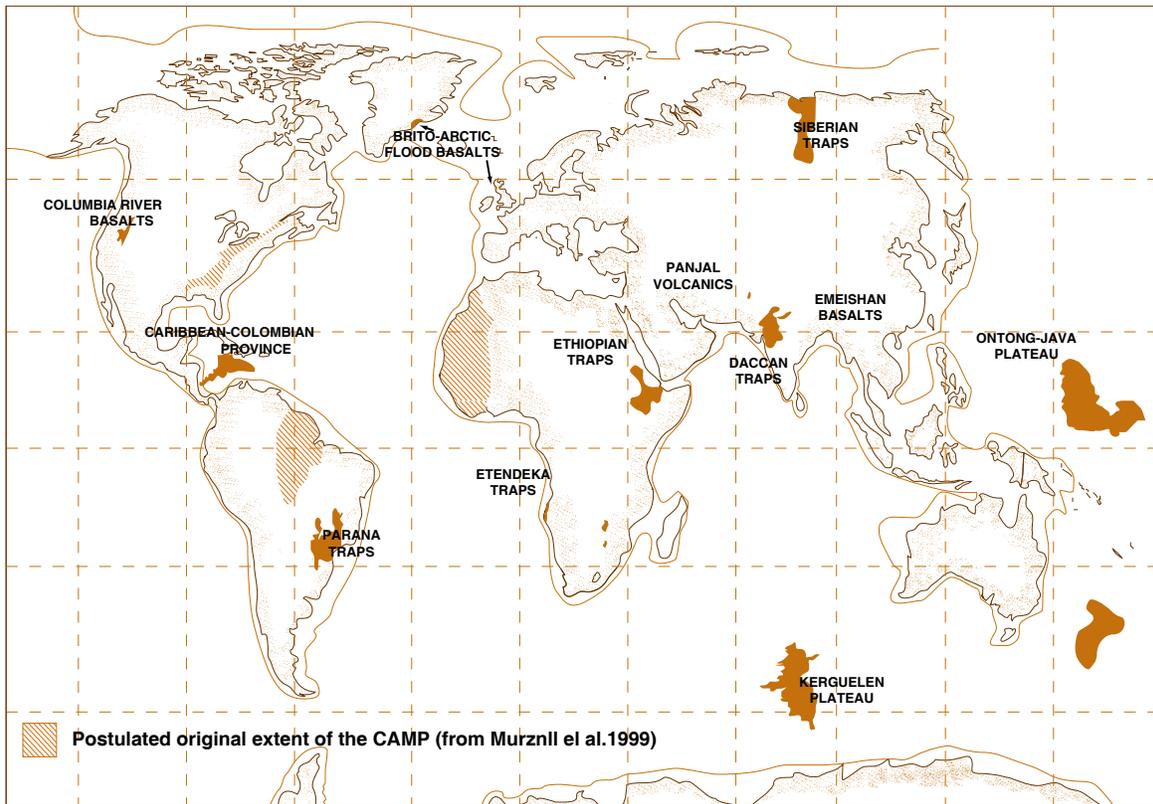
Figure by MIT OCW.

Figure 9-23: Global distribution of continental flood basalts and oceanic basalt plateaus

Figure 9-24 shows, diagrammatically, how an eruption of continental flood basalts might cause a mass extinction (but keep in mind that the caues-and-effect pathways shown in Figure 9-24 are all deductive, so we should not take the diagram on faith.)
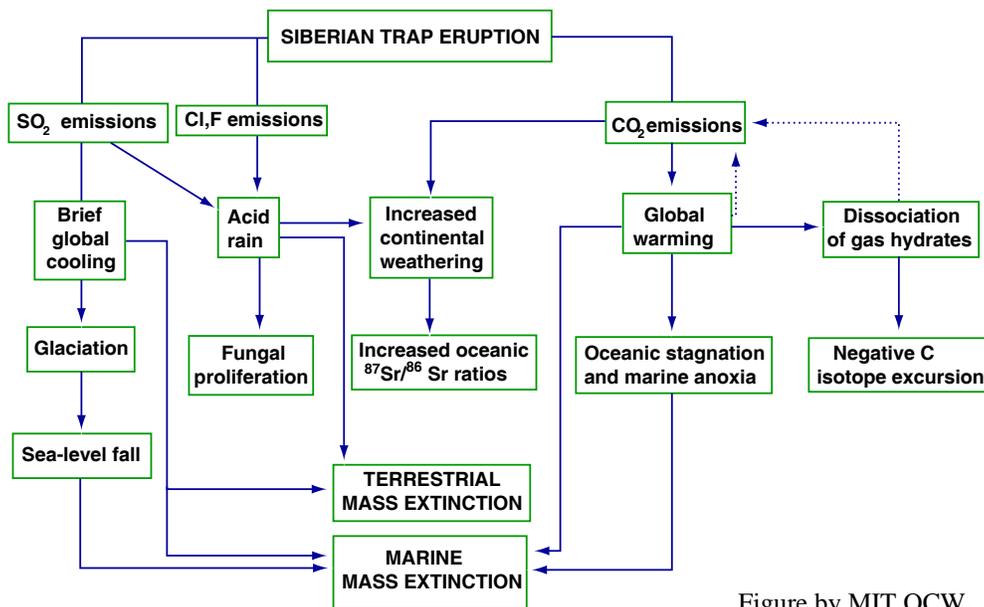
Figure by MIT OCW.

Figure 9-24: Chain of events resulting from eruption of continental flood basalts, with the Siberian flood basalts as an example, leading to mass extinction

6.5 Eustatic (simultaneously worldwide) changes in sea level have long been implicated in mass extinctions. The idea is this: during times of sea-level highstands, large areas of the continents are covered with shallow oceans, affording a great range of habitats for marine organisms. A subsequent large and rapid sea-level fall drains the sea away from the continents, eliminating all of those habitats. (Keep in mind that if sea level falls to the level of the continental shelf break, there is almost no shallow ocean anywhere in the world.)

6.6 The possible effects of each of these possible causes of mass extinctions that might have played a role in the extinctions are highly varied, and to a great extent rather similar from one to another. Figure 9-25 is a tabulation of the possible effects. It's all very deductive, but it gives you an idea of what might have been involved.

Large bolide impact
Reduced light penetration
   Lowered levels of photosynthesis
Increased atmospheric particulates
  Increased albedo
    Global cooling
    Global warming
  Greenhouse warming

Increased cloud cover
  Increased albedo
    Global cooling
    Global warming
Increased atmospheric water vapor and CO_2
  Greenhouse warming

Ozone depletion
  Increased irradiation of surface

Increased abundance of trace elements
  Interference with biochemical processes

Acid rain
  Habitat destruction
  Interference with biochemical processes

"Global" wildfires
  Increased atmospheric particulates (see above)
  Increased cloud cover (see above)
  Increased CO_2 (see above)
  Habitat destruction

Shock heating

Flood basalt volcanism
Reduced light penetration
  Lowered levels of photosynthesis

Increased atmospheric particulates
  Increased albedo
    Global cooling
    Global warming
  Greenhouse warming

Increased cloud cover
  Increased albedo
    Global cooling
    Global warming

Increased CO_2
  Greenhouse warming

Ozone depletion
  Increased irradiation of surface

Increased abundance of trace elements
  Interference with biochemical processes

Eustatic sea-level fall
Reduced shelf area
  Species-area effect
  Habitat destruction

Intensification of climatic gradients
  Heating of continental interiors

Figure by MIT OCW.

Figure 9-25: Effects of proposed causal mechanisms of mass extinctions

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6.7 There have been various attempts at objective evaluation of the correlation between the known mass extinctions, on the one hand, and the various possible causes, on the other hand. It's a truism in science that a correlation, by itself, does not prove cause and effect, but at least if there's no correlation then the given factor could not have caused the mass extinctions. The best such evaluation I have found in the literature is shown in Figure 9-26 (MacLeod, N., 1998, Impacts and marine invertebrate extinctions, p. 217-246, in Grady, M.M., Hutchison, R., McCall, G.J.H., and Rothery, D.A., Meteorites; Flux with Time and Impact Effects: Geological Society of London, Special Publication 140, 278 p. (Figure 1, p. 219)).

6.8 In Figure 9-26, Column A shows, for the entire Phanerozoic, the percent extinction of marine invertebrates, stage by stage. (Note 1: By "stage" here, I mean the official time-stratigraphic unit that is a subdivision of a system, in the official hierarchy of stratigraphic units. Note 2: Owing to the inherent limitations on age resolution, all extinctions occurring during a given stage are placed at the end of the stage.) Column B shows data on major impact events, both direct, in the form of impact structures, and indirect, in the form of geochemical anomalies believed to be caused by the impacts, as well as small, glassy objects, called tektites, which are produced as the vaporized material re-condenses immediately after an impact. Column C shows the occurrence of outpourings of continental flood basalts, and Column D shows three different versions of the curve of Phanerozoic eustatic sea level (see the preceding chapter for more details).

6.9 As shown in Column A of Figure 9-26, at several times in Earth history rates of extinction have been much greater than usual. The greatest mass extinction of all was at the end of the Permian, and the three other largest extinctions were at the end of the Ordovician, at the end of the Cretaceous, and at the end of the Frasnian stage of the Devonian.

6.10 Another way of looking at the occurrence of mass extinctions is to draw a histogram (a kind of vertical bar graph) that shows percent extinction against the numbers of geologic time units that were characterized by that percent extinction. Figure 9-27 shows such a graph, based on stage-level time-stratigraphic units (or parts of stages). Also shown in Figure 9-27 are the so-called "big five" mass extinctions. The clear message from Figure 9-27 is that *there is no real break between the minor, background extinctions, which have characterized most of geologic time, and the larger ones, called mass extinctions*.
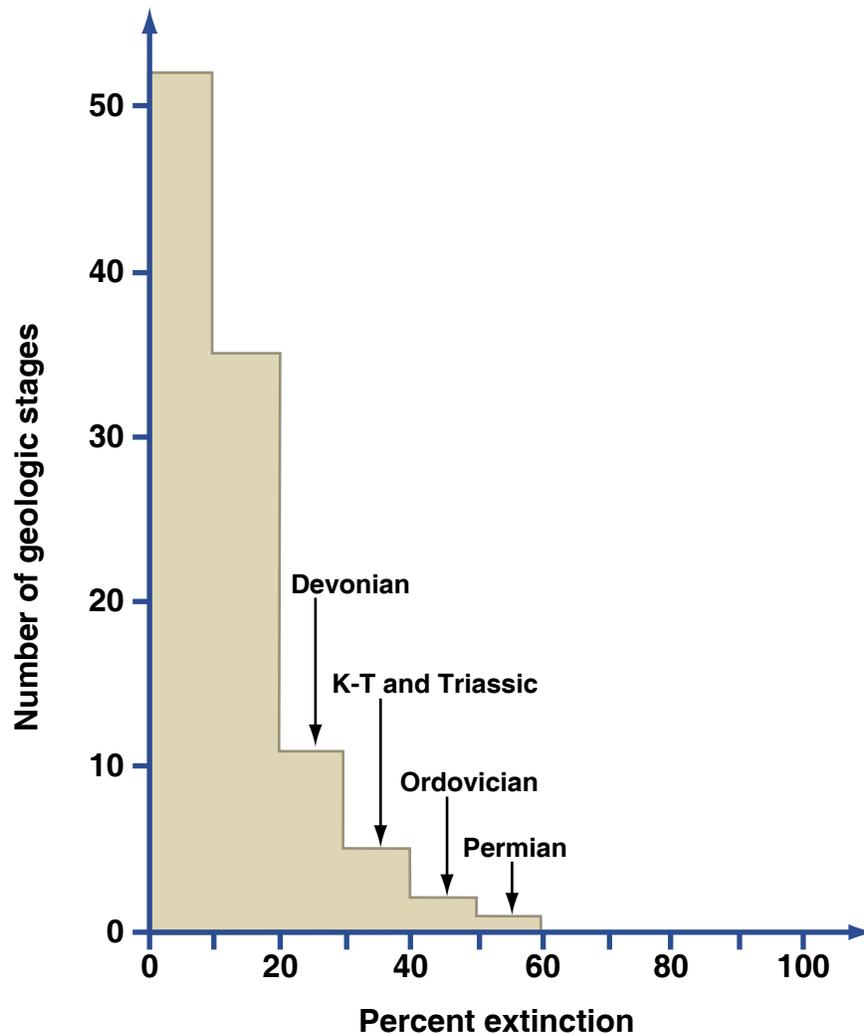
Figure by MIT OCW.

Figure 9-27: Histogram of extinction intensity for fossil genera in 106 time intervals

    6.11 Still another way of describing mass extinctions is to plot a graph (Figure 9-28) that shows percent species extinction, on the vertical axis, against the mean waiting time, in years, between extinctions of the given magnitude. (No details here on how the data are derived and massaged to make the graph.) In climatology, they do the same kind of thing with floods and rainfall events. Note first of all that *the curve is smooth: there's no big vertical step between small extinctions and large extinctions.* Here's an interesting question that arises from a graph like this: how far out on the horizontal axis would you have to go to find the waiting time for a mass extinction that kills all of the species on Earth? At least one researcher thinks that it might be in the ballpark of a billion years— longer than the history of multicellular organisms! An important consideration to keep in mind when using a graph like this is that the actual recurrence time can vary from tomorrow to a billion years plus: the graph shows only the average. (In the same way, the hundred-year rainstorm might be repeated twice in the same year!)

KILL CURVE

Species Kill (Percent) vs **Mean waiting time (years)**

100 million year event
10 million year event
1 million year event
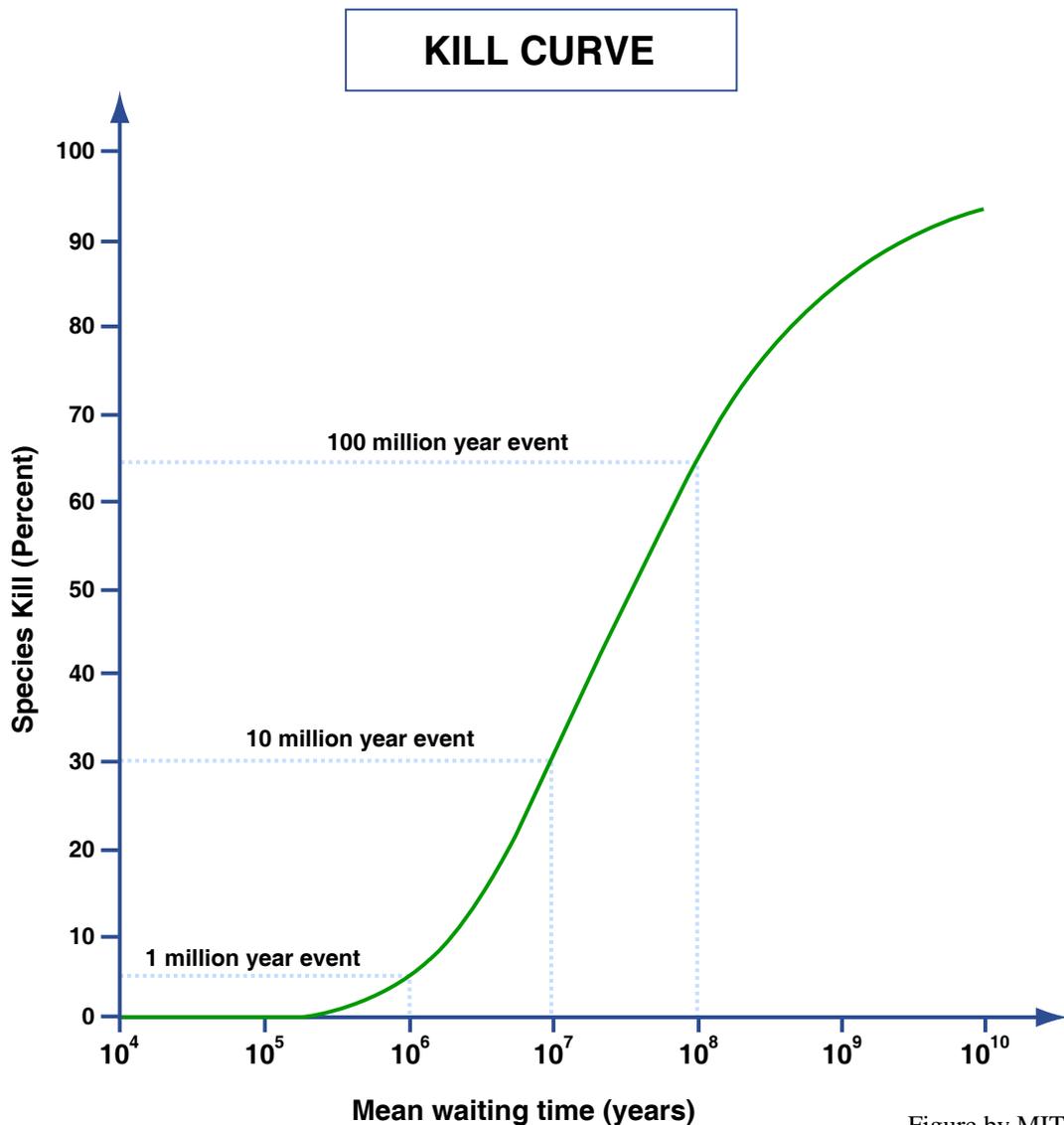
Figure by MIT OCW.

Figure 9-28: Graph showing average waiting time for extinctions of given intensities, based on marine metazoan species

6.10 The results of the comparisons in Figure 9-26 are interesting, and perhaps surprising. There is a clear correlation between the end-Cretaceous extinction and the occurrence of a massive impact—but there is also a general correlation with both volcanic eruption of flood basalts and a sharp sea-level fall. Two of the three other largest mass extinctions were not accompanied by major impacts (or, more precisely, none that are known) but were accompanied by sea-level drops. As shown by Figure 9-29, the correlation between extinctions and flood-basalt eruptions is extremely strong! Does this mean that the eruptions were the direct cause of the extinctions? (It's difficult to construct a scenario in which the extinctions caused the volcanism—but might both have been caused by a third factor?) That seems like a strong hypothesis, but there is still great difference of opinion on that score.
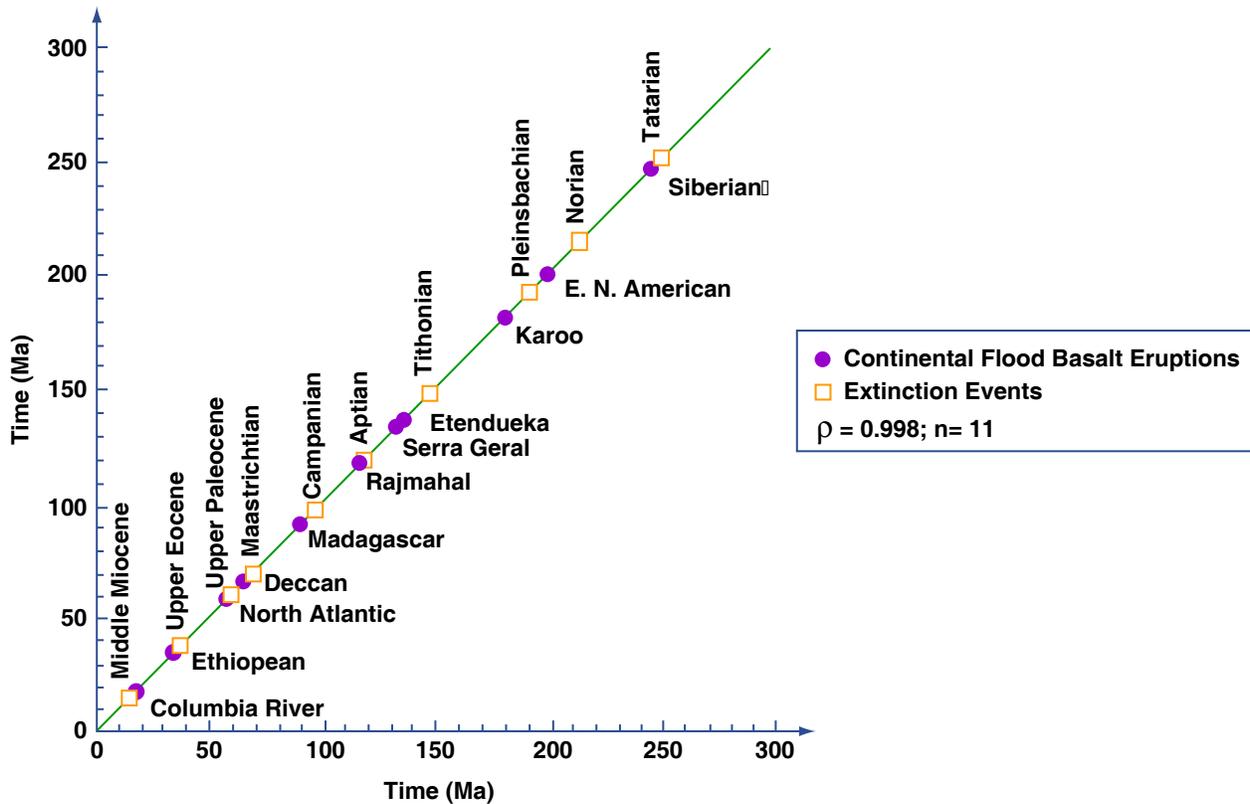
Figure by MIT OCW.

Figure 9-29: Correlation between the ages of large eruptions of continental flood basalts and stages with peaks in extinction intensity, since 250 Ma

6.11 If you read any of the popular or semi-popular literature on the end-Cretaceous extinction, the strong message you would get is that the great Chicxulub impact was the direct cause of the extinction. The hypothesis, first developed in the early 1980s, was based on anomalously high contents of the element iridium in stratigraphic sections around the world at the time of the end of the Cretaceous. Iridium is much more abundant in certain extraterrestrial bodies than in terrestrial materials. Eventually, the culprit impact crater was found, in shallow ocean waters off the Yucatán Peninsula in Mexico, buried beneath younger sediments. Skeptics have pointed out, however, that perhaps the impact was only the final nail in the coffin, in the sense that conditions might already have been made rather unpleasant for life on Earth already, and the effects of the impact pushed so many taxa over the brink of extinction.

7. THE RISE OF LAND PLANTS

7.1 The earliest plants must have been marine organisms. The invasion of the land surface of the Earth by plants was one of the most significant events in the evolution of life on Earth. We don't know when plants first colonized the land surface, because early plants, with their soft tissues, did not fossilize well, especially in the largely oxidizing environment of the land surface.

7.2 Plants must have had to solve a lot of problems to survive on land. Most of these problems involve the atmosphere. Because of the much lower

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density of the atmosphere than of the oceans, plants had to grow against gravity, unless they restricted themselves to low, flat mats. They had to evolve some waterproofing technique, to reduce evaporation from moist outer surfaces. They had to develop ways of circulating water, nutrients, and gases between their upper parts, which extended up into the atmosphere, and their lower parts, rooted in the soil. They had to adapt their reproductive strategies to the atmosphere.

7.3 We can imagine a scenario for the evolution of land plants, starting perhaps with green algae that lived in habitats that were subject to temporary drying. These algae must already have spread to freshwater habitats from their place of origin in the oceans. That could have happened most easily in coastal areas, where brackish-water and fresh-water environments can naturally developed from coastal estuaries and lagoons; you don't need to envision inland lakes that never had any connection with the sea. They might have evolved spores that could be released into the air, where they would have been dispersed much more effectively than in water. There would have been an advantage to projecting part of their structure up into the air, because light levels are higher and uptake of carbon dioxide is more efficient. As the plants emerged into the air, they would have evolved the coatings and transport systems needed for survival. Such a scenario is only speculative, because there's no fossil record on which to base it, only intelligent deduction.

7.4 The earliest spores that are thought to have come from land plants first appeared in the Middle Ordovician—but there are no fossils of plant tissues besides spores until around the middle of the Silurian. The earliest spores of land plants look like those that come from living liverworts. Liverworts, a kind of primitive plant, together with mosses, form the division Bryophyta, one of the main divisions of the plant kingdom. (Botanists use the term "division" for a taxonomic unit that's equivalent to the "phylum" of zoologists.) Indeed, recent molecular evidence suggests that all land plants today are descended from early liverworts.

7.5 We know that a land flora was well established by the end of the Silurian. By that time, vascular plants had made their appearance. Vascular plants are those with tubular structures for efficient internal transport of fluids. Land plants then became much more diverse in the Early Devonian. As the efficiency of vascular systems improved and as structural stiffening material evolved, plants were able to grow taller. By the Middle Devonian, there were fernlike plants with well developed leaves, and trees that grew to over ten meters in height, judging by the tree trunks we see as fossils. By the end of the Devonian, all of the major innovations of land plants had appeared except for flowers and fruit. By Carboniferous time, diversity and sophistication of land plants had increased to a level not exceeded until late in the Mesozoic.

7.6 The rise of land plants, in the Silurian, made for some fundamental changes in the nature of Earth surface processes. As you know, plants play a

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major role in stabilizing the soil surface. Before the establishment of land plants, erosion by running water must have been much more efficient at mobilizing and transporting the products of weathering. On the other hand, weathering processes must have been less intense, other things being equal, because of the important role of plants in promoting weathering. Plants open up rock by invasion by their roots, and the acidic solutions produced by decay of plant material accelerates chemical weathering.

7.7 Another consequence of the stabilization of soils by plant growth is the appearance, for the first time in the geologic record, of meandering rivers. It's well known, from studies of modern fluvial environments, that unless the soils of river valleys are well stabilized against erosion the rivers develop a braided pattern: owing to the freely erodible nature of the bank material, the river is able to spread widely, leading to a pattern of shallow, shifting channels. Only when the banks are stabilized by a combination of fine sediment and plant cover do rivers develop a meandering pattern.

PART V. TIME CORRELATION BY FOSSILS

1 Recall from the chapter on stratigraphy that one kind of stratigraphic unit, time-stratigraphic units, are defined on the basis of time. In order to define and deal with such units in a concrete way, one must be able to make reasonably good time correlations among rocks in different parts of the world. How does one trace the boundaries of time-stratigraphic units? Almost entirely by fossils. This is appealingly simple in principle: evolution has given us a non-repeating sequence of different species in time. But it is difficult in practice, for a variety of reasons. One of the most important reasons is in a way a chicken-and-egg problem: we have to use the same data base—the fossils in the stratigraphic sections around the world—to do two things at the same time: figure out the evolutionary sequence of species, and use that sequence to date the strata. For almost two hundred years now it has been a matter of successive approximations, whereby paleontologists (or, more precisely, stratigraphic paleontologists, those who are more concerned with using the organisms to make correlations than with the paleobiology of the organisms themselves; there is a substantial overlap between the two groups) play off their existing knowledge of the sequence of species, on the one hand, and the stratigraphic record of exposed stratigraphic sections around the world, on the other hand, to continually refine our understanding of the fossil record.

2 The easiest way to appreciate this problem is to imagine yourself to be the first stratigraphic paleontologist ever to take a modern approach to a stratigraphic section. (You might try to assume the role of William Smith, the canal engineer mentioned in the preceding chapter.) You work out a sequence of fossil assemblages in that stratigraphic section and define time-stratigraphic units on the

basis of that succession, and then, armed with that information, go to another stratigraphic section and try to recognize your time-stratigraphic units there by looking at the fossils. Just your common sense tells you that there are factors at work that will make matters difficult for you. For example, the number, duration, and position of diastems (breaks in the record) are likely to be different in the two sections. So, even aside from such things are imperfect preservation or regionality of species, you are likely to find certain of your time-stratigraphic units missing in the new section, and by the same token you will discover new time-stratigraphic units in your new sections, which will force you to redesign your whole scheme of time-stratigraphic subdivision. By now there has been so much work that this effect is felt only at the finest level o time-stratigraphic subdivision, but it will always be with us.

3 Here are some practical things about correlation by fossils:

imperfect preservation
no organisms lived there
breaks in the record
facies control
slow evolution
geographic provinces
finite spread time

4 From the standpoint of the practicing stratigraphic paleontologist, the ideal fossils species is one that spread rapidly into a wide range of depositional environments in all regions of the Earth, built rugged and highly preservable skeletal materials, lived in great abundance, and then became extinct after only a short time. The worst kind of fossil species, on the other hand, is one that evolved to fit a very narrow ecological niche, lived in only a small part of the world, and was so well adapted to its environment that it existed for a long period of geologic time. (Stratigraphic paleontologists refer to fossil species that lived in very specialized and restricted environments, often with a disparaging tone in their voice, as *facies fossils*. Ecological paleontologists, on the other hand, love to see such fossils.) Most fossil species fall somewhere in the middle ground between these two extremes.

5 In general, as you might expect, the finer we try to cut the time cake, the less certain the results. And, of course, it's to be expected that stratigraphers and paleontologists are always trying to push the resolution of the fossil record to its utmost.

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