Chapter 8

Paleoecology

Our task, then, is to identify the remains that lived together, reconstruct the community structure and infer its ecological and evolutionary significance.

James Valentine, Evolutionary Paleoecology of the Marine Biosphere, 1973

ECOLOGY AND PALEOECOLOGY

In the 1960s and 1970s, ecology was one of the hottest ideas in western culture. Everyone was aware of conserving resources and recycling, and many important steps were taken and laws were passed to help our environment. The word “ecology” became such a popular buzzword that it was used far beyond its original biological meaning of the interaction of organisms and their environment. Anything that was good was “ecological,” and advertisers managed to attach the word to all sorts of products that were no friend of the environment. Paleontologists are no less a product of their culture, so they too jumped on this bandwagon. Along with the explosive growth of other paleobiological ideas in the 1970s, the field of paleoecology grew by leaps and bounds as paleontologists tried to extend ecological principles to the fossil record and interpret the paleoecology of fossil assemblages. The pinnacle of this optimistic agenda for paleobiology was epitomized by Valentine's (1973) classic book Evolutionary Paleoecology of the Marine Biosphere, which embraced most of paleontology into the context of paleoecology. Other important books of this period were Ager’s (1963) Principles of Paleocology, Imbrie and Newell’s (1964) Approaches to Paleoecology, Laporte’s (1968) Ancient Environments, culminating with the encyclopedic book, The Ecology of Fossils, edited by McKerrow (1978), along with Dodd and Stanton’s (1981) Paleoecology, Concepts and Applications, and Boucot’s (1981) Principles of Benthic Marine Paleoecology.

As happened with functional morphology, however, much of what was called “paleoecology” was not very original, nor was it testable science. Many studies simply consisted of reconstructing extinct communities as if they were living ecosystems, ignoring many of the real differences between the organisms and their analogues—what Everett Olson called “me-too ecology.” This approach was typified by the book edited by McKerrow (1978), which consists of page after page of pretty pictures of extinct organisms in life position (Fig. 8.1), with few general principles that can be deduced. In his review of this book, Surlyk (1979, p. 446) wrote: “Paleoecology as a science still has a long way to go... It is immensely clear how little we know within the fields of morphological adaptation and modes of life of the great majority of fossil taxa... Paleocology, to be accepted as a modern science, has to shift away from cartoons to much more detailed and quantitative studies.” As Gould (1980, p. 101) put it, “The reconstruction of communities sounds like the right thing to do... But where does it all lead, and why is it being done? Suppose that we could proceed unambiguously, that we could enumerate taxa, determine relative abundances, assign trophic roles, and calculate biomass. At the end, we decide that ancient communities worked much like modern ones. Did we ever doubt it (and if we did doubt it, would this be the way to nurture suspicion)? Community reconstruction will gain theoretical interest when it addresses unresolved questions, but not while it measures success by the fit of individual solutions to modern analogues, and proceeds by enumerating more and more individual solutions.” A number of scientists have leveled similar criticisms (Hoffman, 1979; Hill, 1981; Lewontin, 1982; Paine, 1983; Kitchell, 1985; Benton, 1987; Peters, 1991).

Consequently, the interest in the small-scale aspects of paleoecology has receded since the 1970s and 1980s. Instead, paleontologists have realized that the fossil record is better for examining the large-scale and long-term processes that no biologist can observe. These concepts are now being called “evolutionary paleoecology,” and we will examine some examples at the end of this chapter. Like macroevolution, this large-scale view of ecology is beginning to change the way both neontologists and paleontologists look at the living world, as well as at the fossil record.

Paleoecology is often subdivided into autecology (the behavior of individual organisms and their relation to the environment) and synecology (the ecology of communities...
of organisms and their relationship to the environment). The former is essentially the same as functional morphology, discussed in the previous chapter, so we will not consider it further here. This chapter is chiefly concerned with what is called synecology.

As in functional morphology, the fundamental approach of paleoecology is uniformitarian in nature. We use our understanding of modern processes and modern organisms and communities to attempt to decipher past ecologies. In functional morphology, if the organism has close living relatives, this is easy to do; so too in paleoecology, especially with relatively recent organisms and communities that have many living relatives. For example, a study of Miocene mammalian communities of Africa (Van Couvering, 1980) can largely rely on the modern African savanna as a model, because so many of the organisms are very similar. The use of Neogene microfossils to interpret ancient ocean currents and climates is also straightforward, since most of the species have living relatives with apparently similar tolerances of temperature, depth, and salinity.

But when there are no close living relatives, then the problem becomes more difficult. As in functional morphology, we look for analogues. But is a community of modern bivalves really that good an analogue for an extinct community of Paleozoic brachiopods? Are modern coral reefs really that similar to Cambrian archaeocyathid reefs? In some cases, there simply are no modern analogues. There is nothing on this planet today that approaches the harsh, low-oxygen world of the Proterozoic, with its lack of an ozone layer to screen ultraviolet and its vast sheets of stromatolites with no advanced animals to feed upon them. There is no modern analogue for the early Paleozoic land surface, lacking both vascular land plants to change the pattern of weathering and erosion, and land animals, with their own complex relationships. In these cases, we must use whatever principles of chemistry, physics, and biology seem applicable, but clearly we are in a brave new world where the rules are much less clear-cut.

Still, there are many lines of evidence that can be used in paleoecology, even when modern analogues fail. We can observe the positions of animals with respect to each other, and with the substrate, when they are extraordinarily well preserved. We can look for evidence of associations of organisms. We can look for biogeochemical lines of evidence, especially with respect to the chemical composition of the skeleton and what it indicates. Some of these approaches have been very successful, and we will see their applications in this chapter.

**ECOLOGICAL RELATIONSHIPS**

The term “animal community” is really a very elastic one, since we can use it to describe on the one hand the fauna of the equatorial forest and on the other hand the fauna of a mouse’s caecum.


Ecological communities are merely an epiphenomenon of the overlap in distributional patterns of various organisms controlled primarily by the environmental framework.

Antoni Hoffman, “Community paleoecology as an epiphenomenal science,” 1979

**The Ecological Hierarchy**

Many terms used in ecology are also widely used in common language, so that their precise meaning has been blurred. To clarify this confusion, we will try to define these terms as ecologists mean them. The basic structure of the ecological world is hierarchical in nature, with smaller-scale units clustered into larger, more inclusive units.

The broadest of all categories is the biosphere, the region of the earth’s atmosphere and surface that is inhabited by life. It is a highly abstract term for the biotic envelope of the earth. The biosphere is divided into ecosystems, which are the sum of all the physical and biological characteristics in a given area. Ecosystems are usually very large-scale units, such as the shallow marine ecosystem or the terrestrial ecosystem. Ecosystems are in turn divided into communities, which are local associations of organisms, such as the intertidal community or the savanna community. Each organism in a community has its own habitat, which is the actual physical environment in which the organism lives. An abstract extension of this concept is the niche, which is the sum of all the physical, chemical, and biological limits on the organism, its way of life, and the role it plays in the ecosystem. For example, the habitat of squirrels in the park is the local trees and the ground below them, but their niche is that of a tree-dwelling, nut-gathering small mammalian herbivore. Its community might be the North American temperate forest, which is a subdivision of the temperate terrestrial ecosystem. Even with an example, it is obvious that most of these concepts are not so clear-cut and discrete, since they vary in scale and content. What might be considered an ecosystem in one case might be a community in another context. Ecologists have been battling about the precise meaning of these terms for decades, and some have recommended abandoning them altogether (Peters, 1991). Most ecologists find that, although their absolute definitions are vague, they are useful concepts within the confines of a particular study and so continue to use them.

There are different ways to classify ecosystems, communities, habitats, and niches. One of the simplest is a classification based on environmental factors. For example, in the marine realm (Fig. 8.2), depth of water and the nature of the substrate are frequently used to subdivide the marine ecosystem into smaller parts. The bottom-dwellers (benthic organisms) may live above the range of the tides (supratidal), between them (intertidal, also called littoral) or below the tides but on the shallow shelf (subti-
The depths of the continental slope are called 
**bathyal**, and the broad open ocean seafloor is called the 
**abyssal** plain. A few organisms live in deep oceanic trenches, or the **hadal** depths. Benthic organisms can also 
be classified by how they live with respect to the substrate: 
**infaunal** burrowers, or **epifaunal** organisms that live 
directly on the sea bottom. Some epifauna are attached 
to the seafloor, but other erect large structures (such as coral 
reefs or crinoid stems) that let them filter feed high above 
the seafloor.

This hints at another way of subdividing marine life: 
how they feed. Some infaunal organisms are detritus feeders, 
living on the food extracted from the mud, while others 
simply live in the mud as protection but filter feed by 
sucking in seawater. Still others live on or in the sea bottom 
but crawl around catching prey. Most epifaunal animals 
are filter feeders (also called suspension feeders) but 
many are predators. Marine plants cannot live below a certain 
depth because they need light, so they are usually 
attached to the bottom, or free-floating; there is no real 
infaunal plant life.

Organisms that live in the open waters of the ocean 
(pelagic organisms) can inhabit waters above the shallow 
subtidal shelf (neritic realm) or above the deep ocean 
(oceanic realm). Pelagic organisms can also be classified 
by their way of living in the water. Passive floaters (especially 
microfossils and jellyfish) are **planktonic**, whereas 
active swimmers (especially fish, squids, and whales) are 
**nektonic**.

Of all the problematic concepts in ecology, one of the 
most heavily criticized is the niche. By its very nature, it 
is a vague, abstract concept. Lewontin (1978) points out 
that it is impossible to recognize the niche without the 
organism that fills it. If the niche exists only when an 
organism fills it, is it really a discrete concept, or are the 
definition of the niche and its organism inherently circular?
One can easily imagine an arbitrary “niche” that is unfilled 
such as herbivorous snakes, which do not exist), but without 
an organism to fill it, is there any real meaning or 
explanatory value to the concept? Still, there does seem to 
be some value to the idea of niche. For example, the saber- 
toothed carnivores discussed in the previous chapter 
appear to occupy a distinct niche that has been occupied 
for different times by four different groups of mammals.

At present (and through most of geologic history), that 
niche is unfilled, but the strong tendency for different 
groups of animals to fill it suggests that the concept has 
some merit.

Similarly, the concept of community has been questioned. Traditionally, communities were viewed as tightly integrated entities, with many strong interactions between the members and long-term stability as a unit. But the recent ecological literature seems to show that communities are much more dynamic and ephemeral than traditionally conceived, and that the interactions between the members are much weaker than previously supposed (Hoffman, 1979, 1983; McIntosh, 1980; Kitchell, 1985; Benton, 1987). Hoffman (1979, p. 370) argues that "ecological communities are merely an epiphenomenon of the overlap in distributional patterns of various organisms controlled primarily by the environmental framework . . . There is no intrinsic, biotic mechanism inducing community dynamics that is an inherent trend to maximize a selection value in either ecological or evolutionary time." Today, many paleoecologists are less enthusiastic about the meaning of community reconstructions as exemplified by McKerrow (1978). Kaesler (1982) wrote that "in the early seventies, community paleoecologists were convinced that their science was indispensable to marine ecologists. What could be more important . . . than knowing the history of marine communities through evolutionary time? The answer was loud and clear: 'almost anything.'" Such negative assessments were a bit premature. Although many of the concepts of ecology based on short
time scales are difficult to apply to paleoecology, the fossil record has its own unique contribution to make to ecological theory that could not be discovered from the living biota alone. Such insights are now labeled “evolutionary paleoecology” and will be discussed later in this chapter.

Trophic Dynamics

Another fundamental aspect of the interactions of organisms is energy flow, or “who eats whom.” All living systems ultimately depend on the sun for all their energy, but it is transferred from organism to organism in complex ways. Green plants are the fundamental producers at the base of the food chain, converting the sun’s energy and carbon dioxide into organic matter by means of photosynthesis. Free oxygen is the waste product of this reaction. Most animals are consumers, eating other organisms to get their energy and nutrition and consuming free oxygen to metabolize this food; their waste product is carbon dioxide, which returns to the plants. The primary level of consumers is herbivores, which eat the plants directly. They, in turn, are eaten by at least one secondary level of predators (either carnivorous meat-eaters or invertebrates), and in many food chains, there are multiple levels of predatory animals, each larger than the last and feeding on smaller prey.

Plants, herbivores, and predators are not the only elements in an ecosystem. A variety of organisms feed on others in secondary ways. For example, parasites live off other organisms without killing them (at least not immediately). Scavengers feed on the remains of organisms, and decomposers and transformers (such as fungi and bacteria) also help to break down dead organisms into free organic matter that can be recycled as nutrients, which help living plants and animals grow. In other words, the food chain is better described as a food web, with every organism intricately linked in one way or another with every other organism in the ecosystem (Fig. 8.3). The feeding relationships between organisms is known as trophic structure, or trophic dynamics (from the Greek, “trophein,” to feed).

Until recently, it was thought that photosynthesis and plants were the fundamental basis of the food chain for all life. In 1977, however, a discovery was made which rocked biology (Corliss et al., 1979). Deep-sea submarines diving along the rift valley in the mid-ocean ridges found a previously unsuspected realm of life that does not depend on light, photosynthesis, or plants. These organisms live in the springs of hot water seeping up from the lava-filled vents in the rift valley, and derive their energy from breaking down hydrogen sulfide that seeps up from below. In the place of plants converting carbon dioxide, water, and sunlight into biomass by photosynthesis, these vents are inhabited by bacteria that reduce methane or hydrogen sulfide by chemosynthesis (Cavanaugh, 1985; Fisher, 1990). These bacteria are the base of a food chain that includes foot-long clams, meter-long tube worms, odd crustaceans, and bizarre creatures not seen in any other part of the marine realm. The clams and tube worms lack ordinary feeding structures and digestive systems, since they obtain their nutrition directly from a symbiotic relationship with the chemosynthetic bacteria that live inside them. Detailed analysis of the animals (Tunnicliffe, 1992) has shown that they are unique to this environment (95% of the species and 22% of the families are endemic to vents), and most are evolutionary holdovers from the Mesozoic that have not interacted with the rest of the marine ecosystem in tens of millions of years.

Since these discoveries, paleontologists have discovered a variety of fossil localities that seem to be deep-sea vent faunas, some as old as the Paleozoic. In addition to the hot sulfide-rich vents of mid-ocean ridges, a number of cold, methane-rich vents have been discovered in other regions of the seafloor. These “cold seeps” also have a unique fauna that depends on bacterial chemosynthesis of methane, producing mound-like bodies of carbonate in deep-sea strata. These mound-like carbonate deposits with their peculiar bivalves had long been a puzzle, because they were found in such deep-water deposits, but a chemosynthetic cold seep explanation appears to solve this mystery (Campbell and Bottjer, 1993). [For further information, see the special issue on chemosynthesis in Palaeos, vol. 7(4), August, 1992].

Paleontologists have often tried to reconstruct ancient food webs (Fig. 8.4). Since the Ordovician, the marine seafloor has harbored organisms that appear to occupy many of the same ecological niches in the food web, even if they are unrelated to their living analogue. For example, fish today perform the main roles as swimming (nektonic)
Figure 8.4. Reconstruction of an Ordovician food web. Like modern marine food webs, plants and planktonic animals are the food for a variety of filter feeders (although these are mostly extinct Paleozoic groups.) Unlike modern ecosystems, there are relatively few deposit feeders (mainly trilobites) and very few predators (mainly straight-shelled cephalopods). The multiple levels of crustacean and fish predators that now characterize the ocean was a later development. (From Dott and Prothero, 1994.)

Figure 8.5. The various organisms of the marine realm can be partitioned into ecological niches. In modern faunas, all of the boxes are occupied. In the middle and upper Paleozoic (A), most of the niches had occupants, except for many of the burrowing (infaunal) niches. By contrast, in the Cambrian (B), only a few of the possible ecological niches had occupants. Most animals were suspension or deposit feeders, with almost no burrowers, pelagic forms, or large carnivores. (After Bambach, 1983.)
predators, but before fish with jaws evolved in the Late Silurian, that niche was occupied by nautiloids and eventually ammonoids. The nautiloids were the top carnivores of the Ordovician. But apparently there were not as many different levels of swimming predators among the nautiloids as there are with modern fish, and there were no swimming herbivores until fish occupied that niche much later (Fig. 8.5A). Unlike today, Ordovician corals (from extinct groups, such as rugosids and tabulates) were a minor part of the attached filter-feeding community, with bryozoans, crinoids, and stromatoporoid sponges playing a much larger role than they do today. A number of other niches were occupied by a different cast of players in the Paleozoic (Fig. 8.5A), but the most striking difference occurs in the burrowing, infaunal organisms. Until bivalves (and to a lesser extent polychaete worms and crustaceans) successfully invaded the deeper burrowing niches in the Mesozoic, there were no shallow passive deposit feeders or carnivores, no deep passive suspension feeders, and almost no active deep infaunal feeders of any kind.

If the differences between the Ordovician and modern seafloor are striking, this is even more so prior to the Ordovician radiation. For example, the Cambrian seafloor (Fig. 8.5B) was very different in ecological structure, with very few of the modern niches having occupants. Except for the floating agnostid trilobites and a few soft-bodied forms, there were almost no swimming organisms; the top predator appears to have been the soft-bodied Anomalocaris known from the Burgess Shale, which was only about a meter long. There were abundant shallow deposit-feeding trilobites, but no mobile predators or carnivores on the sea bottom, and very few attached suspension feeders; there was certainly no complex reef community as would appear in the later Paleozoic. The infaunal niches were even more vacant than they were in the rest of the Paleozoic. Thus, the uniformitarian approach breaks down in the Cambrian, when the food web is so much simpler because nothing had evolved yet to fill many of the niches. Community uniformitarianism is even harder to apply in the Proterozoic world, before there were even hard-shelled organisms such as trilobites or especially grazing gastropods. The only common organisms were the cyanobacterial mats that formed huge stromatolites, with no organisms that could feed upon them, let alone predators or scavengers. Essentially none of the boxes in Figure 8.5B (except for the possibility that there were plankton that fed on other plankton) had occupants prior to the late Proterozoic.

The complex food web (Fig. 8.3) that we take for granted today is actually a relatively recent (since the last 500 Ma) invention, which did not exist through most of life’s history. Even more important, its complexity changed dramatically in the Late Proterozoic, and again in the Late Cambrian, before stabilizing into its present guise in the Mesozoic. This kind of large-scale view of ecology would never have been possible without the fossil record, and is one of several examples where paleontology has given us insights that ecologists would never have known about otherwise. We must be careful when we generalize about modern phenomena, such as a complex food web, and assume that it is the obvious or inevitable product of living systems. Through most of life’s history, the food web looked nothing like it does today.

ENVIRONMENTAL LIMITING FACTORS

In solving ecological problems we are concerned with what animals do . . . as whole, living animals, not as dead animals or a series of parts of animals. We study the circumstances under which they do things and . . . the limiting factors which prevent them from doing certain other things.

Charles Elton, Animal Ecology, 1927

Although it is not easy to specify the detailed behavior of an extinct organism, there are certain constraints in the environment that almost certainly applied to the past as they do the present, since these are largely based on invariant laws of physics and chemistry. In many cases, a uniformitarian approach to paleoecology is easily justified, and we can clearly identify which conditions an ancient community must have tolerated and which ones they could not.

Temperature

Temperature is one of the most obvious limiting factors for a number of reasons. Many different organisms tolerate only a limited range of temperature fluctuation. Others can tolerate extreme temperatures and thus have little competition in habitats such as the freezing polar regions. Its most direct effect, however, is on the physiology and metabolism of organisms. Most biological reaction rates vary with temperature, so that metabolism, development, and reproduction typically operate best at an optimal temperature and are dramatically less efficient (or shut down altogether) as temperatures deviate further from the optimum. In many organisms, physiology is governed by van’t Hoff’s rule, which states that for every 10°C of temperature increase up to the optimum, biological reaction rates increase by a factor of 1 to 6 (depending upon species). Although there are exceptions, this increase in biological reaction rates with temperature is a widespread phenomenon. Once the optimal temperature has been exceeded, however, the reaction rate declines rapidly until temperatures are so hot that they become lethal.

Although it is difficult to determine physiological variables directly in fossils, the growth rate recorded in the skeleton can be measured in many different fossil groups (as indicated by growth rings and other characteristics discussed in Chapter 2). Data from living organisms (Fig. 8.6) show that higher growth rates occur with warmer temperatures, so tropical species tend to reach breeding age
earlier and are smaller in body size (Fig. 8.6B). In addition, warm water is more likely to be supersaturated with calcium carbonate, further enhancing the growth of calcified tropical marine life. By contrast, organisms that grow slowly in cold waters breed much later and thus reach larger body sizes. As mentioned in Chapter 3, body size also increases with higher latitude in land animals because larger body size relative to surface area helps conserve heat. In other words, rabbits have larger body size near the poles than they do near the equator.

In local marine communities, temperature is one of the most stable variables, because water has tremendous heat capacity and thermal inertia. Marine seawater in a given area seldom fluctuates more than a few degrees centigrade over the course of the year, so most marine organisms are intolerant of temperature extremes (Fig. 8.6A, top). In the tropics, the fluctuation is even less, but in the temperate latitudes, there may be as much as 5 to 8°C fluctuation due to seasonal changes. When long-term extremes persist for months or years, it can result in a crisis for marine organisms. For example, the unusually warm waters along the Pacific Coast due to the El Niño current decimated the marine life over the last few years, as any Pacific beachcomber or fisherman can attest.

Over the entire world ocean, temperature varies according to latitude, with the warmest temperatures (about 28°C) in the tropics (Fig. 8.6A) and extreme subzero temperatures in the polar regions (since salty seawater freezes at -1.4°C, lower than the freezing point of freshwater, 0°C). Many organisms live in distinct biogeographic provinces based on temperature, particularly in the large water masses of the open ocean. Temperature also varies with depth in the ocean, with surface waters the warmest and deep waters (which typically arise in polar regions, sink to the bottom, and the flow toward the equator) being very cold. For example, most of the deep oceans are bathed in the Antarctic Bottom Water, which forms around the Antarctic continent and then sinks and flows northward along the bottom to as far north as 50°N in the Pacific and 45°N in the Atlantic; this current makes up about 59% of the ocean's water. In the North Atlantic, the North Atlantic Deep Water forms in the Arctic and then sinks and flows south around Greenland, forming much of the bottom water in this region.

Although temperature is a major controlling variable in the marine realm, it is closely related to other variables, such as oxygen content and salinity. For example, the solubility of many minerals (especially calcium carbonate) varies with temperature. Warm water carries a higher concentration of calcium carbonate than cold water, as we mentioned earlier, affecting carbonate skeleton precipitation rates. Conversely, increased temperature lowers the solubility of gases such as oxygen and carbon dioxide, making conditions more difficult for some organisms at high temperature. It is not always easy to tease these variables apart when examining living systems, let alone in extinct organisms.

In the terrestrial realm, temperature is also one of the most important environmental parameters, along with precipitation. Together, they determine the major plant biomes (tundra, taiga, grassland, deciduous forest, desert, and rainforest, and so on), which are largely distributed by the
latitudinal gradient in temperature. Unlike the marine realm, however, terrestrial temperatures are much more variable (Fig. 8.6A, bottom graph). In the continental interiors, where the buffering effect of the ocean is not felt, temperatures can change from scorching to freezing in a matter of hours, such as when an Arctic cold front rolls through the Plains on a hot day. (On one summer day in 1996 in Minnesota, the temperature changed 100°F in a few hours). In addition to being more variable, temperatures on the land can be much more extreme, with subfreezing temperatures covering most of the high latitudes through most of the year, while the seawater in the Arctic or Antarctic remains mostly unfrozen.

Paleoclimatologists seek highly sensitive organisms that are good indicators of paleotemperature. There are many species with very narrow temperature tolerances, so when we find their near relatives in the fossil record, we can make very precise predictions about ancient temperatures. For example, benthic molluscs are arrayed into distinct biogeographic provinces (see Chapter 9) based on temperature and latitude, so a tropical species found much farther north in the fossil record than they occur today indicates that ancient temperatures were higher. Some marine organisms are extraordinarily sensitive to temperature. Coral reefs are restricted to a warm tropical belt between 25° north and south latitude, and individual hermatypic corals live no farther from the equator than 35°. Micropaleontologists have long used the restriction of Cenozoic plankton to water masses of certain temperatures to interpret the distribution of temperatures in the past (Kennett, 1976). For example, the planktonic foraminifer *Globorotalia menardii* is an indicator of tropical conditions, while the thick-shelled *Globigerina pachyderma* indicates cold conditions. In some cases, they respond in even more dramatic ways. Several species (including *G. menardii*, *G. pachyderma*, and *G. bulloides*) switch from right-coiling during warmer interglacial periods to left-coiling during cold glacials (see Fig. 10.4). *Globotruncanana truncatulinoides* changes from highly conical forms in tropical waters to more compressed forms in cooler waters.

In terrestrial ecosystems, there are many species that can be used as paleotemperature indicators. For example, reptiles and amphibians cannot survive where it gets too cold for them to metabolize, so there are definite latitudinal limits on the distribution of such common fossils as crocodilians and turtles. Today, very few reptiles lives north of 70° latitude, and crocodilians are restricted to a belt between 35° north and south latitude. Paleontologists have used this fact to determine terrestrial paleotemperatures and to infer that the polar regions were much warmer in the Cretaceous and Eocene, since they supported a diverse fauna of cold-intolerant reptiles (Colbert, 1964; Hutchinson, 1982; Estes and Hutchinson, 1980). Perhaps the most sensitive paleothermometers, however, are the land plants. Paleobotanists have long used their distribution and physical characteristics to infer ancient climates, especially in locating the ancient tropics by the distribution of thick coal deposits. One of the most sensitive techniques, however, uses the shapes of leaves as paleothermometers (Fig. 8.7). Tropical leaves tend to be larger, thicker, with smooth ("entire") margins and a drip tip, while leaves from cooler climates are smaller, thinner (and possibly deciduous), with jagged margins. The percentage of entire versus jagged margined leaves directly tracks mean annual temperature (Fig. 8.7A), and using that one parameter alone, Wolfe (1978) was able to plot a paleotemperature curve for floras from the Gulf Coast to Alaska (Fig. 8.7B). Recently, Wolfe (1990, 1994) has refined his methods using multiple variables of leaf shape, so that his ability to predict mean annual temperature and the seasonal variation is even more robust and precise.

**Oxygen**

Oxygen is essential for the cellular respiration in animals, so its abundance is another critical variable in marine
and freshwater systems. (Clearly, it is rarely a problem in the terrestrial realm.) Near the surface, the actions of wind and waves constantly mix oxygen in the water, and plants produce oxygen by photosynthesis, so the surface waters are highly oxygenated (as much as 6 ml O₂/liter of water); these conditions are called aerobic. Dissolved oxygen levels drop off rapidly with depth (Fig. 8.8), however, until they reach a threshold of 1.0 ml/l, typically encountered at depths of 400 m. Below this value, conditions are dysaerobic, and typically there is an oxygen-minimum zone in the ocean at depths of about 600 to 1000 m. This low oxygen is caused by the heavy respiration by marine life in near-surface waters, and by the fact that most decay of sinking organic matter occurs at this depth, severely depleting the available oxygen. Below the oxygen-minimum zone, deep ocean waters tend to be well oxygenated, because their flow is mostly derived from the Antarctic and Arctic, where the cold bottom waters form at the surface and then sink, carrying their high oxygen levels with them.

In extremely stagnant, stratified bodies of water, where little exchange occurs between the surface and depths (such as in the Black Sea), bottom conditions can become anaerobic (less than 0.1 ml/l). Such conditions may be devoid of animal life (except for anaerobic bacteria, which cannot tolerate much oxygen), and the extreme reducing conditions produce black shales with pyrite. They also tend to produce stagnant conditions with few or no currents or scavengers, so that extraordinary preservation is possible (see Chapter 1).

Biologically, the oxygen level is critical to many kinds of organisms. Most marine life cannot tolerate low oxygen levels, and lives in the near-surface waters. Corals and cephalopods in particular are known to be intolerant of low oxygen. Some annelid worms, on the other hand, thrive under low oxygen conditions, and thus they tend to be the most numerous animals in the abyssal depths (along with brittle stars and sea cucumbers, which are also tolerant of these conditions).

Lakes can also have depth and oxygen stratification, particularly if they are very deep and have a highly restricted flow. In addition, the bottoms of lakes can have high concentrations of organic matter from decaying plants, so they can quickly become reducing and anaerobic even at shallow depths (as in the typical coal swamp). It is common to find highly stratified lake deposits, with light-colored oxygenated sediments overlying, or even alternating with, anaerobic black muds. Rapid alternation of oxygen levels is particularly characteristic of lakes, since they can fluctuate wildly in these variables (unlike the ocean).

**Salinity**

Salinity is the third most important parameter in marine environments. Measured as the total dissolved salts (especially sodium chloride) per volume of seawater, it is commonly expressed in parts per thousand, or parts per mil (%). Freshwater ranges from 0 to 0.5‰, while brackish water varies from 0.5 to as much as 30‰. Normal seawater salinity is very stable at between 30 and 40‰, whereas conditions between 40 and 80‰ are hypersaline, and greater than 80‰ is a brine. Most marine waters fluctuate very little in salinity around a mean of 35‰. It is slightly higher (up to 36.5‰) in the centers of oceanic circulation gyres in the “horse latitudes” (about 30° north and south latitude), since evaporation is highest there. Conversely, it is slightly lower (as low as 32‰) in polar regions, since the evaporation rate is very low and there is a lot of freshwater runoff. Nearshore regions, especially estuaries and lagoons, are characterized by very large fluctuations in salinity. At certain times there are great flushes of freshwater from runoff, but at other times the runoff is insufficient to keep normal marine waters out of the lagoon or estuary. Hypersaline conditions are usually found in lakes, lagoons or inland seas that have restricted flow of water into them, especially if they are located in the great high-pressure belts of evaporation (between 10 and 30° north and south latitudes), where most of the world’s deserts also occur.

Salinity variations chiefly affect the osmotic regulation of organisms. Some animals and plants have mechanisms regulating the content of body salts when they live in waters that are more or less saline than their internal body fluids; these organisms are known as euryhaline (eury
means "broad" and *halos* means "salt" in Greek). Others cannot do so, and will literally explode or shrivel up if they are in waters that are dramatically different in salinity from their internal fluids; such narrow tolerances characterize *stenohaline* organisms (*stenos* is "narrow" in Greek). Most marine organisms are stenohaline. The few examples of euryhaline organisms (such as oysters, mussels, certain crustaceans, certain foraminifera) are so distinctive that a fauna dominated by them almost certainly inhabited brackish water. Diversity is also strongly related to salinity. The highest diversities are found in normal salinities and drops off dramatically in regions of fluctuating fresh- and saltwater, and even more so in hypersaline waters. Most hypersaline environments can support only extremely salt-tolerant organisms, such as algae, bacteria, ostracodes, and brine shrimp, and have very low diversity.

**Depth and Light**

A fourth important variable in aquatic environments is the depth of the water. Water depth has several effects. The most important is that light penetration decreases with depth, so that photosynthetic organisms (especially algae, phytoplankton, and organisms that are symbiotic with plants, such as hermatypic corals, larger foraminifera, and giant clams) can live only in the upper waters (the **photic zone**). The intensity of light drops off so rapidly below the surface that the base of the photic zone is rarely deeper than 200 m in the clearest tropical waters, and it is usually much shallower (less than 50 m) because particles in the water absorb light. In most marine environments, 80% of the light is absorbed in the upper 10 m of the water column. There is a concentration of marine life near the surface, and the diversity of organisms drops off rapidly with depth.

Below the photic zone is a region of perennial darkness, and thus no photosynthesis or primary productivity takes place. Here, the trophic relationships are much simpler. Nearly all animals (no plants, obviously) feed on detritus, or scavenge dead organisms that sink down, or prey upon these detritus feeders and scavengers. The sparse concentration of suspended food makes filter feeding unprofitable. Although there is less diversity than in the photic zone, recent oceanographic surveys have shown that there is a surprising diversity of detritus feeders.

As depth increases, the loss of light is not the only major change. Temperatures and dissolved oxygen decrease, and other variables (such as salinity and carbonate content) also change. Most ocean waters below the **carbonate compensation depth** (the CCD, or the depth at which carbonate dissolves, about 3000 to 4000 m) are undersaturated with calcite, so that calcareous organisms cannot be preserved. At bathyal and abyssal depths, the pressure of thousands of meters of seawater is so great that most organisms must be adapted to these extreme pressures as well. This is the realm of the bizarre deep-sea fish with their own light sources and the amazing gaping mouths with long, sharp teeth. On the sea bottom, worms, brittle stars, and sea cucumbers tend to predominate (Fig. 16.2).

Paleobathymetry is a very difficult parameter to estimate in the stratigraphic record. Usually the best clue is the fossils themselves, but one must be careful of circular reasoning. One cannot argue that strata are shallow marine deposits because of their fossils and then use that inference to argue that the fossils are shallow marine. Depth can also fluctuate rapidly with changes in sea level, so that a stratigraphic sequence may have been formed at one depth but then overprinted with effects from another depth. For example, an offshore marine deposit may suddenly become shallower or emergent, causing the sediment to be cemented into a **hardground**. Sedimentologists have traditionally used the fining of grain size in deeper and deeper water as a first line of evidence of paleobathymetry, although the presence of coarse sandy turbidites in abyssal depths violates this rule of thumb.

The best fossils for determining paleobathymetry are those that are diagnostic of certain depths. Clearly, tidepool organisms like limpets and mussels indicate intertidal environments, and a high diversity of shelly organisms in fine sands are indicative of nearshore, neritic environments. Finer-grained silts and muds that are low in diversity but have abundant burrows are usually interpreted as deeper and more offshore. One of the most useful groups are the foraminifera, which are strongly depth-controlled. Benthic species are well known to have preferences for certain depths of water (see Chapter 11). Some are associated with shallow lagoons, others with nearshore environments, and still others with offshore shelf, slope, or abyssal depths. The planktonic species that float in the water column above also rain down to the bottom, but they are rare in nearshore waters and progressively tend to dominate the faunas preserved in deeper waters. As depths approach the CCD, the calcareous foraminifera become scarcer, and most of the benthics are made of agglutinated sand grains, which require little calcite. No calcareous species are found far below the CCD, and foraminifera are scarce at abyssal depths (as are most animals).

**Substrate**

Benthic organisms can also be restricted by the nature of the bottom, or substrate, on which they live. For example, most tidepool animals (limpets, periwinkles, barnacles, rock-boring clams) require hard rocky substrates on which to attach, and cannot live anywhere else. Other animals require a soft, soupy, muddy substrate in which to burrow or wriggle along, feeding on detritus. Still others are adapted to the rapidly shifting sands of the surf zone, and thrive by burrowing rapidly once the waves have deposited them on the bottom. Burrowing organisms that filter feed (especially bivalves) do better in coarser sands and silts, because loose muds tend to clog their gills; consequently, there is a much lower diversity of filter feeders on the muddy bottom. Other organisms, such as productid brachiopods, evolved stilt-like spines to prevent their sinking into the soft muddy bottom. Many organisms can live on loose substrates as long as there is one solid piece of rock or shell on
which to attach or anchor. In some environments, these attachment sites become a scarce resource, and every one will be heavily covered and encrusted by colonizers who took advantage. This is especially true of the larvae of marine invertebrates that require a hard surface for attachment, as corals do. Although millions will be released and most eaten by predators, those that survive are largely determined by which ones were lucky enough to land on a hard substrate that wasn’t already crowded with previous tenants.

Unlike temperature, salinity, oxygen, or depth, which are hard to infer from the fossil record, substrate is the only parameter that is directly preservable, since fossils are often entombed in the substrate where they lived. This generalization applies only to organisms that are found in their life habitat; once they have been transported, the sedimentary matrix may have no relation to the substrate originally inhabited by the organism.

In terrestrial environments, substrate (in the form of soils) is one of the most critical biological factors determining what type of vegetation will live (and thus which animal communities can exist). Certain soils, such as the rich windblown proglacial loess clays of the American Plains, central Europe, or China, are extremely rich soils; they are known as the “breadbaskets” of the world. Other soils are extremely poor. For example, the tropical lateritic soils found beneath most of the world’s rainforests are extremely thin and lacking in nutrients. When the rainforest is clear-cut, all the nutrients leave with the trees, exposing a poor soil that quickly turns brick red and rock hard in the sun. Within a few years, it is incapable of supporting much vegetation, let alone another rainforest. Some soils have an unusual chemistry that dictates which vegetation will grow. For example, soils developed on ultramafic rocks, such as gabbros and peridotites, have unusually large concentrations of magnesium (from Mg-rich minerals such as olivine and pyroxene) and calcium (making them alkaline). Consequently, they support a specialized plant community that is tolerant of high magnesium and calcium concentrations in the soil.

Summary

Much is known about how various environmental parameters in living systems constrain the distribution of organisms and ecological communities. In many cases, we can make the uniformitarian assumption and extend this understanding to their fossil counterparts, leading to reliable inferences about the environmental parameters constraining a fossil community. Except for substrate, however, many of these inferences are based on indirect evidence, since there is little direct evidence of temperature, salinity, oxygen content, or depth in a given fossil assemblage. Wherever it is possible to obtain a second line of evidence to test these paleoenvironmental hypotheses (as with stable isotopic ratios discussed in the next section), the reliability of the paleoecological hypothesis can be greatly enhanced.

DIRECT PALEOEKOLOGICAL EVIDENCE

Surprisingly detailed interpretations of past environments are possible, and the fossils themselves acquire much added significance whenever they are studied in the full context of their geologic setting.

Norman Newell, “The nature of the fossil record,” 1959

Although many ecological processes are hard to document in the fossil record, there are also many positive things that we can determine about ancient ecology. In many cases, behavioral patterns and ecological relationships can be reliably inferred from a number of lines of evidence.

Fossilized Behavior

The strongest evidence comes from extraordinary fossilization that actually preserves a behavior. The best source in this topic is Boucot’s (1990) Evolutionary Paleoecology of Behavior and Coevolution, a 725-page book full of examples of fossilized behavior of nearly every imaginable kind. In a short chapter like this, it is impossible to give a sense of the variety of behaviors that have been fossilized, but we can mention a few exceptional cases. There are numerous specimens where symbiosis or commensalism (mutual living together for each other’s benefit) are preserved in fossils, such as the association between the giant Cretaceous inoconlux bivalve *Platyceramus* and the schools of fish that apparently sought shelter inside (Fig. 8.9A). Many different organisms attached to others for a variety of purposes. For example, juvenile productid brachiopods apparently started out life by attaching to a crinoid stem and stayed there until they grew so large (Fig. 8.9B) that they broke free and settled to the bottom, where they rested on the muddy bottom using their spines as stilt. Many organisms attach to others, especially when there is no other substrate available. In addition to familiar cases such as barnacles and encrusting bryozoa, there are more unusual cases, such as the edrioasteroids, which are habitually found attached to large strophomenid brachiopods (Fig. 8.9C). There are many specimens where a parasite is fossilized with its host or a parasite leaves a distinctive scar on the host that can be seen in the fossil.

Even sex can be fossilized. Among the insects found in amber are many cases of individuals caught in the act of copulation (Fig. 8.9D). The cap-shaped gastropod known as the slipper shell, *Crepidula fornicata*, is frequently found stacked one upon the other (Fig. 8.9E). Living *Crepidula* have a very unusual sexual system—the large ones at the bottom of the stack are females and the smaller, younger ones at the top are males. The males have a very long penis that can reach down the stack and fertilize a female far below. When larvae settle, they are attracted to the top of the stack, where they grow up to be male. As the stack becomes larger, the individuals in the middle change sex from male to female. If the top of the stack should be
knocked off, the females remaining on the top can switch back to being male.

Other aspects of reproduction have also been revealed in the fossil record. A Jurassic ichthyosaur from the Holzmaden shales was preserved with a juvenile emerging from the birth canal (Fig. 8.10A), evidence that ichthyosaurs (like dolphins) gave birth to live young (since they could not crawl out on land to lay eggs). A number of examples of dinosaur eggs and nests are known. In the case of Jack Horner’s (1986) famous dinosaur nests from the Cretaceous Two Medicine Formation in Montana,
Figure 8.10. (A) This famous specimen of a Jurassic ichthyosaur from the Jurassic Holdmaiden shale was preserved with a young individual just emerging from the birth canal. (Photo courtesy R. Wild.) (B) An Eocene fish, Mioplosus, died attempting to swallow a Knightia, as preserved in the Green River Shale. (Photo courtesy L. Grande.) (C) This ammonite Plenticeras from the Cretaceous Pierre Shale has a V-shaped row of conical tooth marks from a mosasaur. (From Boucot, 1980.) (D) Two examples of gastropod shells that have been broken or peeled open by predators (probably crabs.) (From Briggs and Crowther, 1990.) (E) Naticid and muricid snails drill beveled holes in their prey. (From Boucot,
some nests show that the young were capable of leaving the nest and feeding immediately after birth, while others (those of the duckbill dinosaur *Matasaura*, the “good mother lizard”) have been interpreted as evidence of parental care, with young that could not leave immediately and were fed by the parents. In the famous Ashfall Fossil Bed State Park in eastern Nebraska, a large herd of the hippo-like rhinoceros *Teleoceras* were entombed in volcanic ash, giving it the nickname “Rhino Pompeii” (Voorhis, 1981). They are preserved exactly as they died, with stomach contents and their last meals in their throats. Perhaps the most touching scene are the baby rhinos, which lie against their mother’s bellies in nursing position, where they died.

Predation is commonly fossilized, both as specimens that have been preyed upon and as predators with stomach contents preserved. Many of the extraordinary fossils in the Lagerstätten discussed in Chapter 1 preserve stomach contents. In the famous Eocene lake deposits of Messel, we can analyze the last meals of many of the animals, because the details of the plant cuticle are delicately preserved. Mammoths that died and were frozen in the Arctic typically have preserved stomach contents (buttercups seem to be favored), and sometimes a mouthful of partially chewed food as well. Many places that are famous for excellent preservation of fossil fish preserve one fish inside another, showing the last meal of the larger fish (Fig. 8.10B). Several ammonite specimens are known that have a distinctive set of conical bite marks arranged in a “V” pattern, suggesting that they were bitten by mosasaurs (Fig. 8.10C).

Specimens such as these, however, tend to be rare exceptions, and not enough examples are known to make broad generalizations or do statistical analysis. Certain kinds of predatory behavior, however, have been studied many times, since there are large samples. Crabs and lobsters can crush mollusk shells with their large claws or break open the aperture and peel it away (Fig. 8.10D). A number of gastropods, especially the murexes (Family Muricidae) and the moon snails (Family Naticidae) prey upon other mollusks by drilling a hole through their shells and then eating their prey inside (Fig. 8.10E). Naticids leave a distinctive beveled drill hole in their prey, and these are very common in the rich shell beds of the Mesozoic and Cenozoic. Numerous studies on naticid boreholes (Kitchell et al., 1981; Kitchell, 1986; Anderson, 1992; Kelley, 1988, 1989, 1991) show that these snails are very stereotyped in their behavior, preferring one valve over the other and certain species over others, and always drilling near the center of the shell. Such data have also been used to assess the long-term changes in predatory behavior over time and the spatial variation in predatory behavior as well (Kelley and Hansen, 1993; Hansen and Kelley, 1995).

Although body fossils are the best direct evidence of behavior, tracks and traces are also valuable clues. We will discuss trace fossils in greater detail in Chapter 18.

**Paleobiogeochemistry**

Although biological evidence of ancient temperatures or salinity conditions are valuable, it is much better when we can find independent evidence to test our estimates of these parameters. Such evidence can come from the chemistry of the shell or bone, and often it tells us much more than we would have expected based on the fossils alone.

**Oxygen**—The most widely used chemical system is oxygen isotopes. Most (99.756%) of the Earth’s oxygen is the light isotope $^{16}$O, which has 8 protons and 8 neutrons. The slightly heavier isotope $^{18}$O, which has 8 protons and 10 neutrons, is normally present in the ocean in rare amounts (0.205%). The two isotopes are compared using a standard formula:

$$
\delta^{18}O = \frac{([^{18}O/^{16}O]_{\text{sample}} - [^{18}O/^{16}O]_{\text{standard}})}{[^{18}O/^{16}O]_{\text{standard}}} \times 1000
$$

The ratio is expressed as $\delta^{18}$O, with more positive (“heavier”) values indicating increases in $^{18}$O and more negative (“lighter”) values indicating increased $^{16}$O. Like the salinity discussed above, oxygen isotopes are measured in parts per thousand (parts per mil, or %) against a standard material, usually calcite in belemnites from the Cretaceous Pee Dee Formation in South Carolina (abbreviated “PDB”).

In 1947, Harold Urey and Cesare Emiliani found that these two isotopes fractionated with changes in temperature. A change of 1 per mil corresponded to an apparent change of temperature of 4.5°C. Water with less $^{18}$O is lighter, so it evaporates more easily than $^{16}$O-rich water; consequently, the clouds are enriched in $^{16}$O and depleted in $^{18}$O. When temperatures are warmer, there is more evaporation and removal of $^{16}$O, and the oceanic waters are thus enriched in $^{18}$O; the carbonate of marine organisms should reflect this change in the ratio. Initially, most studies assumed that the relationship between oxygen isotopes was straightforward. In addition, the carbonate precipitated from seawater during colder temperatures is more enriched in $^{18}$O, while warm water the carbonate is richer in $^{16}$O.

However, there is another complicating factor. When the Earth has polar glaciers (as it did in the late Paleozoic, and has since the beginning of the Oligocene), it turns out that ice volume has an even larger effect than temperature (Fig. 8.11). During non-glaciated times, clouds rain their $^{16}$O-rich water on the land, but it immediately runs off and returns to the ocean, keeping the $^{18}$O/$^{16}$O ratio in the oceans relatively negative. During glacial times, however, much of this $^{16}$O-rich (~30%) water is locked up in the ice caps, making the oceans $^{18}$O-rich by about +1.6%. Thus, the $\delta^{18}$O signal trapped in the skeletons of marine organisms is primarily (about two-thirds) an ice volume signal during glacial times, but more directly measures the global temperature during non-glaciated times. Although the relationship is complicated, oxygen isotopes have become the primary tool of paleoclimatologists
and paleoceanographers for determining ancient temperatures, especially in the oceans. Micropaleontologists and isotope geochemists have collaborated on the analysis of thousands of specimens of benthic and planktonic foraminifera, and have produced a detailed record of climatic change during the Mesozoic and Cenozoic (Fig. 8.12A). When the Deep-Sea Drilling Project began routinely coring Cenozoic sediments on the deep ocean floor, oxygen isotopic analysis became a standard tool in all carbonate sediments. During the glacial-interglacial cycles of the Plio-Pleistocene, the fluctuations of oxygen isotopes are so regular and predictable that oxygen-isotopic “stages” were numbered and used for correlation all over the world oceans (Fig. 8.12B). Paleoclimatologists used oxygen isotopes to estimate the temperature of water masses, and produce oceanic temperature maps of the peak of the last glacial, about 18,000 years ago.

Where temperatures can be assumed to be relatively constant, oxygen isotopes can be used to estimate ancient salinities (Rye and Sommer, 1980; Talbot, 1990). Since clouds are isotopically lighter (more negative Δ18O) than seawater, so is the freshwater and ice on the land that is precipitated from them. Thus, when isotopically light

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**Figure 8.11.** Rain falling on the land (top) is depleted in oxygen-18. When it is locked up in an icecap (bottom), this enriches the ocean in oxygen-18. (From Matthews, 1984.)

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**Figure 8.12. (A)** The oxygen-isotope ratios of the Cenozoic are a good indicator of global temperature and ice volume. (From Miller et al., 1987.) (B) The oxygen-isotopic cycles of the ice ages can be matched up precisely from one oceanic core to another all over the world. (From Shackleton, 1976.)
freshwater mixes with isotopically heavy water of normal salinity, the resulting δ18O will be depressed by as much as -6%. However, it takes an extreme change in salinity to show up in the carbon and oxygen isotopes, and other factors, such as humidity, can complicate the interpretation (Matyas et al., 1996). Stanton and Dodd (1970) and Dodd and Stanton (1975) were able to use oxygen isotopes to interpret the salinity changes that occurred in the Pliocene bay flooding the San Joaquin Valley of California. Salinity was lowest at the north end of the basin where the freshwater influx was highest, and increased to almost normal marine values of 35% toward the south end of the basin (Fig. 8.13). This interpretation correlated with the changes in ribs in the bivalve Anadara, which seemed to vary depending on salinity (Alexander, 1974) (see Chapter 2).

Geochemists continue to find paleontological problems that might be solved with oxygen isotopes. For example, Barrick and Showers (1994) argued that this method could test whether dinosaurs were warm- or cold-blooded. The latter have poor temperature regulation, and thus a great difference in temperature between the core of the body and the extremities, while warm-blooded animals keep the temperature nearly constant throughout the body. Since δ18O strongly responds to temperature, the difference in oxygen isotopic ratios in bones found in the core of the body versus bones from the extremities should be able to test this hypothesis. Barrick and Showers (1994) examined the δ18O of Tyrannosaurus and other dinosaurs and found less than 4°C difference, suggesting they were warm-blooded. However, if dinosaurs were cold-blooded animals that maintained constant body temperature due to their size and reduced surface area, this would have produced the same result.

Carbon—The second most commonly used geochemical system is carbon isotopes. Most of the carbon (98.89%) in the Earth is in the form of 12C, which has six protons and six neutrons. The heavier stable isotope, 13C, which has an extra neutron, constitutes about 1.11% of the Earth’s carbon. Like oxygen isotopes, these two carbon isotopes cycle through the atmospheric, oceanic, and terrestrial environments, and are found in atmospheric CO2, in carbonate rocks, and in organic materials. Any material with carbon in it—shells, bone, wood—will contain one or both of these isotopes and can be sampled and measured as oxygen isotopes are. The formula for measuring δ13C is similar to the oxygen isotope formula given above, with appropriate substitutions of 13C for 18O and 12C for 16O.

A number of different processes control the ratios of 13C to 12C, so there is no simple relationship with temperature and ice volume, as there is for oxygen isotopes. Nevertheless, several factors are known to affect carbon isotope ratios in the oceans, as recorded in the carbonate of marine fossils. Organic materials tend to be low in 13C, so when they decay they release a lot of 12C, causing the value of δ13C to decrease (become more negative, or lighter). Deep ocean waters are a major source of 12C-rich organic materials, so that when deep waters are brought to the surface during upwelling, it causes the δ13C to shift to more negative values. Thus, changes in δ13C in the oceans usually reflect changes in oceanic circulation and, by extension, oceanic productivity. Combined with oxygen isotopes, these two systems can be valuable tools in interpreting paleoclimates and paleoceanography.

Because carbon is the most abundant element in most living systems, carbon isotopes have been used in many other contexts besides paleoceanography. For example,
the carbonate in terrestrial soils also contains a distinctive ratio of $\delta^{13}C$, which can change due to a number of effects (Cerling, 1984; Cerling et al., 1989). Carbon isotope studies have shown that grasslands and savannas did not appear until about 7.5 Ma (Cerling, 1992; Cerling et al., 1993; Wang et al., 1994; Quade et al., 1994; Quade and Cerling, 1994). The shift in $\delta^{13}C$ is apparent not only in the soil carbonate, but even in the teeth of the fossil mammals from these beds. This has led to an interesting paradox: horses, camels, and other mammals with high-crowned teeth for eating gritty grasses appear as early as 15 Ma, but the geochemical evidence shows quite clearly that there were no extensive modern-type grasslands until 7 million years later. If there were no true grasslands at 15 Ma, what were these animals eating that required such high-crowned teeth? This puzzle has still not been resolved.

Another important discovery derived from carbon isotopes is the great oceanographic change at the Paleocene/Eocene boundary. At that time, a dramatic decrease of 3% in marine carbon isotopes shows that a major circulation change took place; oxygen isotopes and other paleoclimatic signals show that it was a peak of warming as well (Kennett and Stott, 1990, 1991; Stott, 1992). The carbon isotope shift even shows up in the soil carbonate of the Bighorn Basin of Wyoming (Rea et al., 1990; Koch et al., 1992), as well as in the teeth of the fossil mammals found in these beds. The exact timing of the abrupt climatic warming at the Paleocene/Eocene boundary can be seen in the terrestrial record, and its effect on the mammals can be precisely calibrated.

Scientists continue to find new paleoecological uses for carbon isotopes. For example, chemosynthetic organisms that live in hydrothermal vents and cold seeps have a $\delta^{13}C$ that is considerably lighter (more negative) than shallow marine invertebrates that depend on a normal food chain (Ríos et al., 1992); their ratios of strontium to calcium and magnesium are also distinctive. If one suspects that a peculiar assemblage of animals might be a chemosynthetic vent fauna, the isotopes provide a test.

In recent years, paleobiogeochmistry has become one of the most powerful tools in paleoecology and paleoclimatology, so a modern paleontologist needs to know more geochemistry than we have room to discuss in this chapter. Within a few years, there will be other novel applications of geochemical techniques to solve paleoecological problems. One of the best aspects of paleobiogeochmistry is that it provides an independent test of ecological predictions based on behavioral biology or morphology, allowing much greater scientific rigor in paleoecology. In some cases (such as the paradox of horses with high-crowned teeth before there were modern grasslands), it has led to some surprises, so our classic hypotheses need to be rethought.

**SOME ECOLOGICAL IDEAS THAT HAVE BEEN APPLIED (AND MISAPPLIED) TO FOSSILS**

We see, in the vastness of geologic time, events that bear superficial similarity to phenomena of local populations—and we assign a similar cause without realizing that the extended time itself precludes such an application.

S.J. Gould, "The promise of paleobiology as a nomothetic evolutionary discipline," 1980

One of the biggest problems in applying ecological principles to ancient deposits is the matter of scaling. Most phenomena in ecology operate on a time scale of minutes to years, and rarely on a scale of decades to centuries. To the paleontologist, this is an unsolvable problem. When we try to fit most fossil assemblages into modern ecological models, we have completely ignored the implications of "millions and millions of years." Much of what has been written about paleoecology based on modern ecology is interesting, but utterly inapplicable to the fossil record for this reason. In this section we will look at some ecological concepts that seemed to apply to the fossil record, only to be undermined by problems of scaling or taphonomy or other aspects of fossilization that biologists seldom encounter.

**Food Pyramids**

An important aspect of trophic dynamics is the rate at which energy is transferred between organisms. In the process of feeding on other organisms, animals must use some of that energy for their own growth and metabolism. Consequently, for a given total weight (biomass) of plants, there must be a smaller biomass of herbivores and even a smaller biomass of predators. This is known as the food pyramid (Fig. 8.14A). The slope of the pyramid reflects the fact that the transfer of energy from level to level is relatively inefficient. Some portion is unavailable as food to the next level, since it is used for growth, metabolism, and other phenomena and is not incorporated into the tissues of the organisms at that level (and thus not available to be eaten by the next level). This means that a given biomass of plants necessarily supports a much smaller biomass of herbivores, and predators are necessarily fewer than their prey. If there are multiple levels of predators, the loss of energy at each level becomes more and more attenuated, so that a top predator (like a hawk, or a lion) is necessarily much more rare than its prey items. Typically, such top predators are not only scarce, but must range over large areas in order to find enough food, which further prevents them from reaching large population sizes.

But the marine food pyramid (Fig. 8.14B) is inverted. It appears that there is less plant biomass than there are consumers. How could this be? It turns out that generalizations about food pyramids work well as long as the rate of
Figure 8.14. (A) The energy pyramid for a normal ecosystem has much more producer biomass (P) than herbivores (H), and even less carnivore biomass (C; TC = top carnivore) and decomposer biomass (D). Each bar represents the total energy flow through a given trophic level. The darker portion of each bar represents energy locked up in the biomass in the area studied, while the lighter portion represents energy that is lost through respiration or movement downstream and out of the study area. (B) In a marine ecosystem, the energy pyramid appears to be inverted, because the plants at the base (phytoplankton) have such short generation times compared to their consumers (zooplankton) that they are replaced much faster than the consumers. The numbers are biomass in g/square m for the water column and seafloor beneath one square meter at the sea surface. (From Raup and Stanley, 1978.)

Overturn at each level is similar. Marine systems, on the other hand, are based on planktonic algae that have a much higher rate of overturn than the planktonic and nektonic animals that feed upon them. At any given time, the plant biomass is small, but it is replaced so rapidly that it more than keeps up with the consumers, which have a much longer generation time. By contrast, the lifespans of terrestrial plants (especially trees and shrubs) are as long or longer than the animals that feed upon them, so their biomass is much more consistent with the normal pyramid shown in Figure 8.14A. Turnover rate and generation times are important considerations when comparing the biomass at each level of a food pyramid.

The concept of food pyramids has important implications that paleontologists have tried to apply to understanding extinct organisms. For example, if the predator is warm-blooded, or endothermic (like a bird or mammal), it uses most of its food (about 90%) just to keep warm, burning its fuel to produce metabolic heat. Endothermic predators (like birds or mammals) are much less efficient than cold-blooded (ectothermic) predators (like crocodiles), which use very little of their food for metabolism and can feed infrequently (think of how long a snake takes to digest a single meal). This means that endothermic predators must eat more often, and eat much more biomass per predator, than ectothermic predators. Thus, a larger biomass of prey species is required for each predator (Fig. 8.15). In terms of food pyramids, the slope of a system with ectothermic predators is much steeper than one with endothermic predators, since a given biomass of prey supports fewer of the former.

Bakker (1972, 1977) used this relationship as an argument that dinosaurs were endotherms. He pointed out that modern communities with endothermic predators have a very low predator/prey ratio, typically 1:10, or 10%, so the food pyramid has a very shallow slope. By contrast, fossil communities with ectothermic predators will have many more of them, so the predator/prey ratio will be close to 4:10, or 40%, and the slope will be steep (Fig. 8.15). Bakker then looked at the predator/prey ratios in fossil terrestrial vertebrate communities. Early Permian communities, for example, had many predators (chiefly the big fin-backed mammalian relative, Dimetrodon), but by the late Permian, their predator/prey ratios were very low. Mesozoic dinosaur-dominated communities had very low predator/prey ratios (always less than 5%, and typically even lower), as did Cenozoic communities with mammalian predators (which were undoubtedly endothermic).

However, the story is not so simple. As a number of critics (Thulborn, 1973; Charig, 1976; Tracy, 1976; Farlow, 1976, 1980; Beland and Russell, 1980) have pointed out, the distinction between endothermic and ectothermic predator/prey ratios is not so clear cut. The more data are considered, the more the two ranges of ratios overlap, so that there are ectothermic predator communities with low ratios and endothermic predator communities with high ones. More important, it is very difficult to find any suitable modern analogue for an ecosystem with a large ectothermic predator (and no endothermic predators) on which to base this comparison. Practically the only examples are communities where lizards are the top carnivores, and they don’t begin to approach the dinosaurs in size. (Some of Bakker’s examples used spiders as top predators, and they’re not even vertebrates.) For it turns out that body size is an important variable that needs to be considered. A huge predator (such as a large carnivorous dinosaur) loses body heat very slowly, simply due to the fact that it has a large body mass relative to its surface area (discussed in detail in Chapter 2). Consequently, it may have been warm-blooded with a stable body temperature...
simply due to its size, and may not have needed endothermy to keep active and catch prey. A tyrannosaur may have gotten by with a few kills a month (as does a large crocodile) and still have been an active predator.

Another important consideration is taphonomy. In Chapter 1, we pointed out that the process of fossilization introduces all sorts of biases and distortions to the death assemblage that is actually preserved and fossilized. If the predator is much more or less likely to be fossilized than its prey, then the predator/prey ratio in the fossil record would be meaningless. Bakker (1977) argues that both the predatory and prey dinosaurs are of similar body sizes, so their bones should be preserved with the same probability. However, there are plenty of examples that force us to question this assumption. The famous Cleveland-Lloyd Dinosaur Quarry, in the Upper Jurassic Morrison Formation near Price, Utah, yields almost entirely predatory *Allosaurus*, with few prey specimens. Either the predators were cannibals, or this quarry is not yielding a reliable predator/prey ratio. Cleveland-Lloyd may have been a predator death-trap, like the famous Pleistocene La Brea tar pits in Los Angeles (Fig. 1.5B), which preserve far more predators (saber-toothed cats, dire wolves, bears, lions, coyotes) than they do prey (mammoths, mastodons, horses, camels, ground sloths). Apparently a single trapped prey animal, struggling for freedom, attracted many predators and scavengers, who all became trapped and died. Further examples like this cause us to doubt whether the ratios preserved in museum collections can be used at all. One could easily explain the low predator/prey ratio in dinosaurs by arguing that the predators may have lived in upland areas, away from floodplains where fossilization takes place, or were usually too clever to get caught. By contrast, the stupid, lowland-dwelling sauropods and duckbills were much more likely to get caught in floods, and when they died, their bones were much more likely to be buried in the floodplain. Since we cannot rule these possibilities out, the entire data base of predator/prey ratios has to be regarded with suspicion as evidence of past biology.

**Community Succession**

A very popular concept in ecology is known as succession, or the regular changes that take place in a community as it becomes established and matures to a stable endpoint. Perhaps the most familiar example, found in every introductory science book, is the forest succession. It starts when a wet habitat (such as a lake) is gradually invaded by pioneer marsh plants and filled in with sediment. Once the ground becomes drier, the marsh plants are replaced by intermediate plants, such as grasses or shrubs, and ultimately by larger trees, forming the stable climax community. Unless fire or other disturbance disrupts this sequence, successions will naturally tend to the stable climax community. In other cases, succession occurs when a habitat is disturbed—by fire, volcanic ash, flash flood, or the retreat of an ice sheet—and the bare ground is taken
Figure 8.16. Examples of the successional stages of four ancient reefs, showing the vertical succession of the reef biota. (From Walker and Alberstadt, 1975.)

over by pioneering weeds, and then (if there is no further disturbance) by larger plants that can root more deeply and withstand environmental fluctuations better than the opportunistic weeds. All these cases are examples of autogenic, or internal, self-driven, successions, where the activity of the early members of the community alters the environment and allows the later members to dominate. There are also cases of allogenic succession, or replacement, where the sequence of organisms and/or communities is due to changing external factors, such as climatic changes, salinity changes, sea level changes, or other non-biological factors.

Paleontologists have long sought examples of succession in the fossil record. Raymond (1988) described the sequence of ancient plant communities that occurred as a Pennsylvanian deltaic complex progrades from brackish marine to freshwater to terrestrial environments. Johnson (1977) described a case where one group of pioneering brachiopods, which were tolerant of muddy bottoms, provided a hard substrate on which other brachiopods could attach. Stanton and Dodd (1981, p. 436) show an example of a succession of a coral attached to a bryozoan attached to a scallop shell. Apparently, corals do not attach to scallop shells directly, but must have a bryozoan substrate.

The best-documented examples of succession are ancient reef communities (Fig. 8.16). Walker and Alberstadt (1975) illustrated a number of cases where the pioneers are soft-substrate tolerant organisms (often crinoids, brachiopods, or bryozoans during the Paleozoic) that stabilized the substrate, followed by a colonization
stage, where larger colonial animals take over once the substrate is hard and stable. These are then replaced in the diversification stage by a complex community consisting of not only the colonial organisms (corals, sponges, archaeocyathids, or whatever is important at the time) but also a variety of organisms that live in the sheltered backreef environment (including delicate bryozoans, brachiopods, crinoids, and other lagoon dwellers). Most Paleozoic reefs are capped by a domination stage, where a single organism (typically stromatoporoid sponges) completely takes over the reef as a stable climax community. Walker and Alberstadt (1975) show seven examples of Ordovician, Silurian, or Devonian reefs that seem to follow this pattern, as well as the rudistid bivalve reefs of the Cretaceous, which have some similarities (Fig. 8.16).

These examples can legitimately be called true autogenic successions, because the stages are clearly very short in duration. Reefs in particular are good examples of success because they trap the early stages of their history in their layers (but see Copper, 1988, for some problems and caveats). However, most stratigraphic sequences represent much longer time scales than the days to years that are required for normal ecological successions. Each bedding plane may be separated by gaps that represent hundreds to thousands of years, so a series of communities through a thick stratigraphic sequence represents thousands to millions of years of accumulation. The years to tens of years of ecological phenomena are lost in the gaps between beds (Schindel, 1980). Gould (1980) points to examples of "successions" in the Ordovician studied by Bretsky and Bretsky (1975), or in the Devonian by Walker and Alberstadt (1975), where the "pioneer," "intermediate," and "climax" communities are separated by tens of feet of strata and probably spanned millions of years. As Gould (1980, p. 103) put it, "I don't deny that certain patterns of faunal change, observed over millions of years in geological sequences, offer some interesting analogies to classical succession. But the scale is all wrong; they cannot represent the process itself, and attempts to force such sequences into a successional mold obscure a phenomenon [sic] that may be new and revealing." Bretsky and Bretsky (1975) talk about "opportunists" that persist through many feet of strata, but Gould (1980) points out, "opportunists cannot persist for millennia if the concept of self-induced change has any meaning." Such "successions" are more likely caused by allogenic factors, such as repetitive systematic changes in sea level, than they are by internal autogenic forces that cause true biological succession. In the terminology introduced earlier, these are examples of community replacement and have little to do with succession as recognized by most biologists. Such patterns of replacement may be interesting in their own right, but they are not equivalent to the biological processes involved in autogenic succession. Most paleontologists and ecologists (e.g., Gould, 1980; McCall and Tevesz, 1983) agree that "only in exceptional circumstances does the fossil record preserve the evidence of ecological succession. There is also agreement that most large-scale evolutionary patterns previously attributed to ecological succession are not. Both global extinction and speciation are embedded in the pattern, and the time scale is too long" (Kitchell, 1985, p. 98).

**Competition**

Another important principle of ecology is competition, or the interaction between two organisms striving for the same thing (food resources, space to live, mates, light, or whatever resource is limiting). Many examples of competition have been documented among living organisms. One of the central concepts that has come from these observations is Gause's competitive exclusion principle, which states that whenever two organisms try to occupy the same niche, they will tend to subdivide the niche, or one will drive the other out completely. For example, if two species of birds inhabit the same trees, they will subdivide the tree canopy into different habitats or seek different food resources. In other cases, competition is so severe that only one species will occupy the niche without the intervention of outside forces. For example, the exposed rocks of the intertidal zone are a limited resource exploited by a variety of barnacles, algae, limpets, periwinkles, and mussels (Paine, 1966). However, this balance between species would not exist were it not for predators, since mussels are capable of growing much more aggressively and crowding the others out. Only when predators keep the population of mussels in check can there be a higher diversity of intertidal life.

In recent years, the entire concept of competitive exclusion has been challenged by ecologists (Heck, 1980). Nevertheless, paleontologists have tried to explain aspects of the fossil record by competition and competitive exclusion. Once again, we run into the problems of scaling and duration. Most competitive interactions in biology take place in a matter of hours to years at the most, a time frame too short to see in the fossil record. At best, we would see one group replace another within the span of one bedding plane, and not a protracted replacement that stretches over many feet of strata and millions of years.

One of the classic cases of competition was the alleged replacement of brachiopods by bivalves during the Mesozoic. As early as 1857, Louis Agassiz wrote, "Every zoologist acknowledges the inferiority of the Bryozoa and Brachiopoda when compared with the Lamellibranchiata [bivalves] . . . Now if any fact is well established in Paleontology it is the earlier appearance and prevalence of Bryozoa and Brachiopoda in the oldest geological formations, . . . until Lamellibranchiata assume the ascendancy which they maintain to the fullest extent at present." Simpson (1953, pp. 115-116) wrote, "A major feature of the fossil record, and correspondingly of the history of life, is that of succession and replacement of one group of organisms by another . . . Some mollusks and some brachiopods are enough alike so that there is a certain relation between the expansion of one phylum and contraction of
the other." In their classic paleontology textbook, Shrock and Tavenhoef (1953, p. 352) attributed the decline of the brachiopods to their "constitutional inaptitude to compete successfully with the Mollusca under changing conditions."

Gould and Calloway (1980) looked at the problem in detail and found no evidence of competitive displacement. First of all, clams and brachiopods do not compete in any real sense. Nearly all brachiopods (except the inarticulates) live epifaunally on the seafloor, and the majority of bivalves are infaunal, burrowing beneath it. Although these two groups may both filter the same seawater for food, they are not competing for space. In fact, during the Paleozoic, the brachiopods dominated the offshore shelf environments, while clams were restricted to nearshore habitats. Through most of the Paleozoic, the two groups lived without either one increasing at the expense of the other; brachiopods maintained a high level of diversity, and bivalves a lower one. Then the great Permian extinction decimated brachiopods (especially productids, orthids, and strophomenids, which became extinct) much more severely than bivalves. In the Triassic aftermath, the bivalves recovered, while the brachiopods did not, for reasons we do not yet fully understand. The spiriferid brachiopods survived into the Triassic but then disappeared in the end-Triassic event, leaving only rhychoconellid and terebratulid brachiopods to survive until the present, as well as the "living fossil" inarticulates. If Vermeij (1977, 1987) is right, the increased predation on epifaunal shelled organisms in the Mesozoic made the exposed brachiopods (such as spirifers) more vulnerable than the burrowing bivalves, or the rhychoconellid and terebratulid brachiopods, which today hide in crevices in rocks. Clearly, the idea that the brachiopods and bivalves could compete with each other for tens of millions of years before one pushed the other out is an unwarranted extrapolation from ecological processes happening in a geological instant, and is not supported by a close analysis of the data. In Gould and Calloway's (1980, p. 393) words, "Instead of acting as competitive antagonists, continually pressing upon each other during hundreds of millions of years, brachiopods and clams may have behaved more like Longfellow's 'ships that pass in the night'— 'only a signal shown and a distant voice in the darkness.'"

Perhaps the strongest case for competitive exclusion in the fossil record involves the barnacles. The chthamaloid barnacles are commonly known to be outcompeted by the balanoid barnacles in modern intertidal habitats. Stanley and Newman (1980) suggested that the replacement of chthamaloids by balanoids in the Cenozoic might also be due to competitive exclusion. However, Paine (1981) challenged this conclusion on several grounds: (1) the smaller chthamaloids would be less susceptible to predation and can live in the refuge of the higher intertidal area; (2) their supposed "competitive exclusion" is largely maintained by differential predation in the tropics, and in temperate regions, where disturbance by bulldozing limpets is more important than predation, the chthamaloids live much lower down in the intertidal zone, and outcompete the balanoids; (3) there is no real evidence in the fossil record that such competition took place in the past. Newman and Stanley (1981) acknowledged many of Paine's criticisms, but still argued that competition was the primary factor. Palmer (1982) and Branch (1984) also argued that predation and environmental factors were more important than competition. Kitchell (1985) regarded the fossil record of the two groups as too poor to provide a conclusive test.

Another classic example of alleged competitive exclusion is the displacement of the archaic mammals known as multituberculates, and the primitive primates known as the plesiadapids, by the invasion of the rodents from Asia to North America. All three groups were small herbivorous mammals with chisel-like incisors, adapted for living in trees and gnawing fruits and nuts. Multituberculates and plesiadapids flourished in North America in the Paleocene (multituberculates even go back to the Jurassic), and when rodents arrived in the early Eocene (55 Ma), the other two groups went into gradual decline. The last plesiadapids occurred in the middle Eocene (47 Ma), and the multituberculates finally expired in the latest Eocene (35 Ma). Kraitse (1986) found that the evidence was consistent, if not conclusive, for the rodents displacing the multituberculates, and Maas et al. (1988) came to a similar conclusion for the plesiadapids being replaced by rodents. Nevertheless, the three groups overlapped by about 20 million years. If this was true competitive exclusion, it operated at an excruciatingly slow pace.

Other classic examples of competitive exclusion have not fared as well. For example, the synapsid ancestors of mammals were allegedly driven to extinction in the Late Triassic by competition from the early dinosaurs. However, Benton (1983, 1987) argued that the data were inconsistent with competition, especially over the long span of the Late Triassic. The odd-toed perissodactyls (horses, rhinos, tapirs, and their relatives) were supposedly outcompeted by the even-toed artiodactyls (pigs, camels, cattle, deer, and their relatives) during the Cenozoic, but Cifelli (1981) found no evidence to support this. In summary, competitive exclusion is an important ecological process, but in most cases it operates too rapidly to be seen in the fossil record.

**EVOLUTIONARY PALEOECOLOGY**

"Evolution cannot be understood except in the frame of ecosystems.

Ramón Margalef, Perspectives in Ecological Theory, 1968

The history of organisms runs parallel with, is environmentally contained in, and continuously interacts with the physical history of the earth.

George Gaylord Simpson, "Historical Science," 1963
If we cannot observe many important ecological processes in the fossil record, what is left for paleoecology? Paleontologists have responded by looking at phenomena that operate only on the large scale of millions of years and are invisible to ecologists of the living biota. This approach was first labeled “evolutionary paleoecology” by Valentine (1973) and has become one of the most exciting areas in paleobiology. We have already discussed one example of the process—the marine community structure and food web before the Ordovician was much simpler than anything living today. Such a discovery forces us to re-examine the assumptions about ecology based on the modern world, because through most of life’s history, food webs were not as complex as they are today. What other large-scale ecological trends can we find in the fossil record, and what do they tell us about our ecological theories based on the modern world?

Phanerzoic Diversity and the Three “Evolutionary Faunas”

One of the first questions that Valentine (1969, 1970, 1973) posed was, “What is the pattern of diversity of life?” Collecting the data then available on the total number of fossil species throughout the Phanerzoic, Valentine produced a curve showing that diversity was low through most of the Paleozoic, but accelerated rapidly in the Mesozoic and Cenozoic, with the highest levels of diversity occurring at present (Fig. 8.17A). Valentine viewed this increase as a result of greater specialization and ecospace utilization as life became more sophisticated.

Raup (1972, 1976a, 1976b) was not convinced by Valentine’s analysis and suggested a number of non-ecological reasons why the curve might have the shape it does. For example, the shape of the diversity curve closely correlates with the curve for total rock area, suggesting that the diversity at each time horizon might be an artifact of the total rock available to be sampled for fossils (Fig. 8.18B, C). The younger the rock, the more likely it will be exposed at the surface, and the less likely it has been destroyed by erosion. All of these might contribute to its fossils being more abundant and diverse.

Another possible bias is the fact that well-exposed rocks tend not only to yield more fossils but also to attract more attention from paleontologists (Sheehan, 1977). This suggests that the apparent diversity curve might actually be a curve of paleontological interest and activity (Fig.8.18D). Such a suggestion is supported by “monographic bursts” that occur when the publication of major monographs appear and increase the number of published species. For example, publication of major monographs on Permian brachiopods by Cooper and Grant suddenly increased the apparent diversity in the Permian.

A third possible bias is the “pull of the Recent.” Diversity might rise so sharply to its modern-day maximum because the modern biota is much better preserved and contains soft-bodied animals that seldom fossilize. If those animals have just one previous occurrence in the fossil record, their range is automatically extended backward into the Cenozoic and occasionally into the Mesozoic. Thus, there may not be many more fossils at each level in the Mesozoic or Cenozoic, but these soft-bodied animals are counted as present at time intervals when they are not fossilized, simply by the fact that they occur at least once in the fossil record and are still living.

Since all these biases tend to produce curves that correlate with the apparent diversity curve of Valentine, Raup (1972, 1976a, 1976b) suggested that the true shape of diversity may not be slow acceleration to a modern-day
maximum. Instead, he argued that life diversified rapidly in the Cambrian and Ordovician, filling most of the niches and then reaching an equilibrium state (Fig. 8.17B). This curve is almost the diametric opposite of Valentine’s (and also of the empirical data). How could we test which of these is closer to the truth? Just counting the species all over again doesn’t solve the theoretical dispute behind the data. Is there any other way of measuring diversity besides species counting?

Bambach (1977) proposed a novel way to test these alternatives. He studied 386 well-sampled, well-preserved fossil communities throughout the Phanerozoic and tabulated their species diversity. In this manner, he could address the question of whether diversity of a typical Cambrian or Ordovician community is actually less than a Cenozoic community, or whether this is an artifact of the compilation of the data (Fig. 8.17C). Bambach found that there was an increase in diversity through the Phanerozoic (contrary to Raup), but not nearly as extreme (only 4 times as large, not 10 times as large as suggested by Valentine).

While these disputes were raging in the literature, Jack Sepkoski was working on a new, much more accurate tabulation of the total number of families in the fossil record (finally published in 1982). His tabulations (Sepkoski et al., 1981) suggested that the truth was between the two extremes proposed by Raup and by Valentine (Figs. 8.17D, 8.19). Diversity had indeed increased rapidly in the Cambrian and Ordovician and then reached a plateau through most of the Paleozoic (as suggested by Raup). However, after the great Permian extinction caused a dip in diversity, it began to increase in the Mesozoic and

Figure 8.19. Sepkoski’s (1977, 1978) factor analysis of Phanerozoic marine diversity. He found that the marine fauna was composed of three main components: a “Cambrian fauna” that dominated the Cambrian and declined after the Ordovician; a “Paleozoic fauna” (Pz) that dominated the Ordovician through Permian; and a “Modern fauna” (Md) that was present in the Paleozoic, but dominated the Mesozoic and Cenozoic. (From Sepkoski, 1981.)
Figure 8.20. Sepkoski's "three evolutionary faunas" (see Fig. 8.19) are shown here separated so their individual diversity histories are clear. Also shown are cartoons of the major groups that dominate each "evolutionary fauna." (Modified from Sepkoski, 1981.)
nated in the Ordovician through Permian was composed mostly of articulate brachiopods, crinoids, rugose and tabulate corals, stenolaemate bryozoans, and nautiloids and goniatitic ammonoids. This faunal dominance was completely rearranged by the Permian extinction, and during the Triassic a "Modern Fauna" arose, dominated by bivalves, gastropods, echinoids, crustaceans, bony fish, sharks, and eventually marine mammals—the creatures that still populate the oceans today.

Paleontologists have long known that there are fundamental differences between the Cambrian world, the rest of the Paleozoic, and the Mesozoic-Cenozoic, but could not describe this difference in precise quantitative terms. What originally seemed to be an insoluble dispute over the overall shape of diversity has turned into an insight into the fine structure of the last 540 million years of evolution. It would not have been as apparent without the large-scale tabulation of diversity of Sepkoski (1982), which in turn would never have been stimulated without the original debate between Valentine and Raup over Phanerozoic diversity.

**Onshore-Offshore Trends**

In the process of analyzing the total diversity of the Phanerozoic and breaking it down into evolutionary faunas, Sepkoski found that his data base could produce other interesting results as well. For example, the elements of the modern faunas (especially bivalves and gastropods) were present in the Paleozoic, but did not dominate in most environments. Sepkoski and Miller (1985) looked at the depth and substrate information associated with these faunas and found that there was an ecological separation between these two evolutionary faunas. During the Ordovician, the brachiopod-crinoid-bryozoan-coral-rich "Paleozoic fauna" was dominant in the more offshore habitats, but bivalves and gastropods tended to dominate the inner shelf and nearshore regions (Fig. 8.21). In essence, the Permian extinction did not simply wipe out the Paleozoic fauna—it also meant that the offshore shelves were stripped of brachiopods and other "Paleozoic fauna" groups, and when life returned in the Triassic, those offshore habitats were taken over by bivalves and gastropods.

Marine ecologists have long argued whether the nearshore environment, with its high variability due to tides and storms, or the deep ocean, with its long-term stability, would be better places for new taxa to originate. The fossil record is the ideal place to test this hypothesis. Dave Jablonski and Dave Bottjer (Jablonski and Bottjer, 1983; Jablonski et al., 1983; Bottjer and Jablonski, 1988) looked at the time and place of the first occurrence of numerous groups in the fossil record, plotting their position on the offshore-nearshore gradient. A number of scientists had noticed that novel marine communities tended to occur in nearshore habitats first, while archaic forms often persisted in deeper waters, and Jablonski and Bottjer found that this was indeed true: new communities did indeed arise in the nearshore, and tended to displace older com-

Cenozoic well beyond Paleozoic levels (as Valentine had suggested, but more in line with the orders of magnitude suggested by Bambach).

Sepkoski (1977, 1978, 1979) went beyond looking at the total diversity, however. He broke down the diversity curve into components, using a multivariate method known as factor analysis. Sepkoski found that the total diversity separated into three distinct components, which he called "evolutionary faunas" (Fig. 8.20). His "Cambrian fauna" was a distinct assemblage dominated by trilobites, inarticulate brachiopods, and primitive echinoderms and mollusks. The "Paleozoic fauna" that domi-
munities as they expanded to the more offshore habitats. However, the reasons why this is so are less obvious (Jablonski and Bottjer, 1988). It may be that nearshore habitats, with their high variability, are stressful and drive organisms to adapt to new conditions and speciate. Finally, onshore communities may just be more resistant to extinction, so that even if novelties arise with equal probability at any depth, those that occur nearshore have a better chance of surviving and spreading out.

**Tiering**

Total diversity and community composition are not the only fundamental differences between the Cambrian, Paleozoic, and Modern faunas. Ausich and Bottjer (1982, 1985; Bottjer and Ausich, 1986) looked at another aspect of ancient communities: how many different levels, or tiers, above and below the sea bottom did they occupy? They found that during the Cambrian, the trilobites, brachiopods, and archaeocyathids occupied only the surface of the seafloor (or dug shallow burrows), and few were tall enough to filter feed more than a few centimeters off the bottom (Fig. 8.22). By the Ordovician, however, crinoids were feeding over a meter above the sea bottom, exploiting an ecological niche that was unavailable until organisms grew tall. Other stalked echinoderms and tall bryozoans, as well as corals, were capable of filter feeding at intermediate levels, allowing for a fine-scale subdivision of the water column several meters above the bottom. Through most of the Paleozoic, however, there were no deep burrowers. In the late Paleozoic and Mesozoic, bivalves with long siphons, as well as a variety of worms and crustaceans, began to dig deep burrows as much as meter below the seafloor, exploiting yet another ecological niche that was unoccupied until organisms with deep burrowing adaptations came along. This multiple tiering was temporarily disrupted by the Permian extinction, but returned in the Triassic. Giant crinoids declined after the Jurassic, so the highest tiers of the Paleozoic have not been duplicated in the Cenozoic. The deep burrowers, however, have maintained their Permian levels of tiering.
When we look at modern marine communities, we would never suspect that ecological complexity was ever very different in the past. But the analyses by Bambach mentioned in the early part of the chapter and the analysis of tiering show that we cannot think of the pre-Permian world in the same terms as the present—the complexity of modern communities had not yet evolved.

**Escalation**

Another phenomenon that is invisible to modern ecologists was proposed by Vermeij (1987) in his fascinating book *Evolution and Escalation: an Ecological History of Life*. Vermeij has long studied phenomena such as the history of predation on mollusks by other species that peel them open, or drill their shells, and noticed that when new predators arose, the prey species tended to evolve defenses (thicker shells, smaller apertures, defensive spines, or swimming ability) that protected them. Vermeij called this phenomenon **escalation**. It is analogous to the arms race during the Cold War—each development in armaments on one side tended to provoke a defensive reaction and stronger armaments by the other. The best example of this phenomenon is Vermeij’s (1977) “Mesozoic marine revolution” discussed earlier in the chapter. During the Triassic, a number of new predators—marine reptiles, bony fish, crustaceans, and starfish—appeared that had superior methods of crushing shells. None of these animals existed in great abundance in the Paleozoic, so there was no pressure on bivalves or brachiopods back then to protect themselves. But when the seafloor suddenly became more dangerous for shellfish in the Triassic, the bivalves, gastropods, and echinoids that could burrow, or protect themselves with spines, or swim away, survived. Epifaunal brachiopods and bivalves and unprotected gastropods and echinoids went into decline. In short, the arms race between predators and prey escalated during the early Mesozoic, and the world changed in such fundamental ways that the old “Paleozoic fauna” could never return to its former glory (even if it had done better in the Permian crisis).

The phenomena of escalation and tiering together suggest reasons why Sepkoski found that diversity increased since the Paleozoic and why the modern fauna is so different from the Paleozoic fauna. The presence of new ecological niches in the Mesozoic (especially the deep burrowing tiers) allowed for greater diversity than in the Paleozoic, and the escalation of predators required that the prey become more diverse in their adaptations to escape new forms of predation. These ecological phenomena, which are only visible on the scale of millions of years, would never have been suspected by an ecologist looking only at the living world. These are the types of insights that “evolutionary paleoecology” has produced, and they give us a whole new way of thinking about ecology.

**CONCLUSIONS**

Paleoecology flourished in the 1970s as paleontologists jumped on the ecology bandwagon and tried to apply modern ecological principles to the fossil record. Then it foundered when it became apparent that many ecological phenomena operated on scales that were invisible at the scale of geological events, and when “me-too” paleoecological reconstructions led to few original insights. In recent years, however, “evolutionary paleoecology” has begun to show that there are many phenomena—community diversity, evolutionary faunas, onshore-offshore origination trends, tiering, escalation—that are invisible to the ecologist working only in the modern time frame. These insights promise not only to revitalize paleoecology but also to challenge many of the assumptions of modern ecology as well, leading to a much richer and more realistic picture of how life works.

**FOR FURTHER READING**


