Science B-16: The History of Life

Lab 3: Communities through Time

INTRODUCTION AND OBJECTIVES

The science of paleontology, as was stressed in previous labs, contributes much more than a simple description and classification of fossils. Among other things, we can not only gain insight into what ancient organisms looked like, but also what they did during their lifetimes: where they lived, what they ate, how they moved, and what other animals they potentially interacted with. We can also "watch" as different groups of organisms replace each other in particular environments through time. A Paleozoic lagoon, for example, was inhabited by very different animals than a Mesozoic one, which in turn is very different from one of today.

This lab exercise takes the organisms you learned about in the first lab and places them in a temporal and ecological context. We will be tracking three different environments through time: reef, marine soft-bottom, and terrestrial, and we will be looking at how the taxonomic makeup of organisms living in these environments has changed during the course of the Phanerozoic Eon. You should come away with a set of mental images of the characteristic organisms that lived together at different periods in Earth history. Once again, please ***read this handout before coming to section***. Also, ***bring your copy of Lab 1 with you***, for you will be looking at many of the same organisms again, and you will need to be able to recognize them in a different context. A copy of the geologic time scale (on the cover of your sourcebook) will also be helpful.

PALEOECOLOGY

"Behind the history of every sedimentary rock there lurks an ecosystem..." (Edward Deevey)

In last week's lab, you learned how to determine the depositional environment in which a sedimentary rock formed. Once the environment of deposition is determined, paleontologists can then look at the fossils preserved in the sedimentary rock and try to determine how those organisms fit into their physical surroundings. The modern science of **ecology** examines the relationships of organisms with their environment and with other organisms in the same **community** - a group of organisms that live together in the same environment. The field of **paleoecology** applies modern ecological principles to the fossil record in an attempt to reconstruct ancient communities. Because it is far more difficult (though not impossible) to address questions of organism interactions in the fossil record, paleoecology can be more realistically defined as simply the study of the relationships between ancient organisms and their environments.

The raw data of paleoecological research are the fossils preserved together within individual layers of rock. One can never be quite sure, however, that these organisms actually comprise a true community. There are many other reasons that could account for associations observed. The transportation of mollusk shells, for example, from many different areas onto a beach where they accumulate together results in a false association of species. This particular source of error is relatively easy to identify with a bit of experience, but others are not so obvious. For this reason, **paleocommunities** are more conservatively defined as recurring groups of fossil organisms that may or may not correspond to real communities. An even more encompassing term is the **assemblage**, which only implies a collection of organisms that lived in roughly the same environment in roughly the same time frame. This is probably the more accurate word to use when describing the majority of ancient "communities".

The most common questions asked by paleoecologists revolve around the **mode of life** of ancient organisms. Where did they live? What did they do? How and what did they eat? These questions are addressed using a combination of methods described in Lab 1 (e.g., comparison with modern relatives or functional analogs). There are several different ways to describe and group organisms according to their modes of life, and these methods are usually done simultaneously.

The first and most fundamental is the distinction between mobile and immobile. (Another is the distinction between solitary and colonial organisms, life modes that were discussed in the first lab.) **Mobile** animals are those that are able to move around - swim, crawl, burrow, etc. Immobile organisms, called **sessile**, are restricted to living in the same spot for their lifetimes either because they are physically rooted or cemented, or because they have no means of locomotion. Oysters, for example, are sessile animals because they are permanently cemented to a substrate, while snails are mobile because they crawl or glide along a surface.

One can also address the question of where the organism lives with respect to the **substrate -** the sediment accumulated at the bottom of the body of water. Organisms may either live in the water column or on the bottom, and those that live on the bottom can live on the surface of the sediment or buried within it. Among **benthic** organisms (those that live on the bottom), we can further distinguish between those that prefer hard substrates (barnacles grow on rocks) and those that prefer soft substrates (some clams burrow in the sand).

Another useful means of characterizing organisms relies on the feeding strategies they employ. Animals that eat other animals are called **carnivores** or **predators**, while those that eat plant matter are **herbivores** or **grazers**. Many animals do not fit into either of these categories, relying instead on bits of dead organic matter (**detritus**) for their main food source. Animals that eat detritus mixed in with the sediment are called **deposit feeders**. Conversely, **suspension feeders** filter suspended particles of detritus out of the water column and ingest them. There are other categories that can be defined also, depending on what environment you are looking at.

A final concept that has proven useful in paleoecologic analyses is that of the **guild**. A guild is a group of organisms that are in competition for the same resource. This resource is usually food, but could also be space or light, particularly for plants. A familiar example of a guild system based on feeding strategies for the African savannah could be as follows: photosynthesizers (which produce their own food) include a variety of grasses and shrubs, herbivores are the antelopes, zebras, and giraffes, predators are the leopards, lions, and hyenas, and scavengers are vultures, hyenas, and lions. Membership in a particular guild is independent of taxonomy (e.g., zebras and giraffes are not closely related, but both eat the same food), and a given species may be included in more than one guild at the same time (e.g., the hyena is both a carnivore and a scavenger). It should become apparent throughout this lab that the concept of guilds can be rather plastic and subjective, yet affords a very useful approach to comparing communities through time.

EXAMPLES FROM THE ROCK RECORD

Simply learning about environments of deposition and how organisms adapt to and live in those environments is not enough to understand the history of life on Earth. Sedimentary rocks themselves do not "tell" history. A Cambrian shale looks much the same as a Cretaceous one or a Pliocene one. The physical laws controlling its deposition do not change with time, and thus the properties of the rock itself do not change through time. Likewise, the basic strategies that organisms employ to live in particular environments do not change significantly either. There were deposit feeders, predators, and sessile suspension feeders in the Cambrian, just as there are now. The objects that do tell history are the fossils. The organisms that occupy given positions in communities change dramatically over time, and this is what gives us a temporal component, an "arrow," to life's history.

Even the earliest geologists recognized that fossils preserved in older rocks were very different from those in younger ones. The three great divisions of the Phanerozoic were recognized based on the distinctive suite of fossils contained in each, and these were separated by very clear, natural breaks in the record. The first major turning point was the Precambrian-Cambrian boundary, marked by the first appearance of abundant, skeletonized animals. This signaled the beginning of the Phanerozoic Eon. Two other major turnovers in taxonomic composition occurred at what we now recognize as the Permian-Triassic and the Cretaceous-Tertiary boundaries. These are the divisions between the Paleozoic, Mesozoic, and Cenozoic Eras, recognized by the mass extinctions of marine invertebrate species (96% and 75%, respectively) that occurred at each. To get a feel for the historical nature of life's history, we will look at characteristic assemblages of each of these eras and observe how organisms in three different environments changed over the course of the Phanerozoic.

SOFT-BOTTOM ASSEMBLAGES THROUGH TIME

Communities of shallow-water, marine organisms that live on soft substrates (mud, silt, and sand) are perhaps better represented in the fossil record than any other community. The edges of the continents inundated by ocean waters are sites of relatively continuous deposition of sediments, and thus the chances for burial and preservation are comparatively good. You will see, after reading this account and looking at the specimens provided, that general feeding strategies have remained constant since the Cambrian but the taxonomic membership of animals in each feeding "guild" has changed dramatically.

Paleozoic

The beginning of the Paleozoic was marked by an explosive radiation of skeletonized invertebrate phyla (the "Cambrian Explosion"). Prior to this time, trace fossils created by unknown soft-bodied organisms provide the primary evidence for multicellular life. Some of the earliest, skeletonized, soft-bottom inhabitants were the trilobites, probably deposit feeders scavenging bits of detritus on the sea floor. Many kinds of early trilobites lived in association with suspension feeding brachiopods, an occasional ancestral gastropod, and several groups of problematic, shelly fossils that may be related to molluscs. The spectacular soft-bodied fauna of the Burgess Shale in British Columbia provides a snapshot look at the dazzling array of early invertebrates that lived in the Cambrian oceans.

It appears from this material that all the traditional feeding guilds of the later Phanerozoic were occupied already, even the predators, as evidenced by the 2 foot long *Anomalocaris*. Later Paleozoic soft bottom communities were characterized by a great diversity of brachiopods, trilobites, crinoids, solitary rugose corals, bryozans, and infrequent bivalves and gastropods. Benthic animals lived predominantly on the surface of the sediment as opposed to buried within it. Evidence suggests that burrowers were not particularly common, and those that did exist were restricted to shallow depths. Predators were mostly active swimmers and included the giant eurypterids during the Silurian, uncoiled nautiloid cephalopods during the Early and Middle Paleozoic, coiled nautiloids and ammonoids later on, and fish. Fossils of these animals are found preserved in sediments with bottom dwellers, and so paleontologists need to be able to recognize them as transitory members of bottom communities.

Mesozoic

The close of the Paleozoic brought about a dramatic change in soft-bottom dwellers. Most notably, the trilobites became and the once numerous brachiopods dwindled significantly. Mesozoic assemblages are characterized by a growing diversity of molluscs and crustaceans, with brachiopods, crinoids, and bryozoans still present but subordinate. Some Mesozoic bivalves grew asymmetrically (like the rudists) so that one valve became large, heavy, and cup-like and the other became a flat lid. Some animals (e.g., the oyster *Exogyra*) lay free in the sediment with the lid on top, filtering food particles from the water. Such a shape was successful unless the clam was overturned, for they had no means of righting themselves. This way of life was common until the Cretaceous, when "biological bulldozers" like burrowing bivalves, worms, and crustaceans became more active and abundant. These animals churned the sediment more completely and to greater depths so that large, free-lying organisms were no longer stable in the soft sediment. Because of constant overturning by bioturbators, this life mode is no longer represented today. Classic Mesozoic fossils are the ammonites, found almost ubiquitously in a wide range of marine depositional environments. Again, many of these are swimming, open-ocean animals that are only preserved in soft-bottom assemblages when they die and fall to the sea floor.

Cenozoic

The rise of molluscs and crustaceans that began in the Mesozoic continued to accelerate in the Cenozoic. Predatory forms became more common, and the diversification of fast, deep burrowing bivalves and gastropods with thick shells and spines is presumed to be in response to the rise in predators. Fish are also important components of Cenozoic soft-bottom ecosystems. Sponges, bryozoans, and assorted worms comprise the rest of the bottom dwellers. Flowering plants in the form of seagrasses entered the marine realm late in the Cretaceous and spread during the early Cenozoic. Their appearance created a new habitat for marine animals, making them important members of shallow-water, soft-bottom communities

REEF ASSEMBLAGES THROUGH TIME

Although most people are aware that tropical areas today are characterized by coral reefs, few realize that there have been reefs of some kind present on the earth for nearly all of the history of life. Even before the origination of large animals, bacterial reefs formed in shallow tropical seas. The term reef is here defined as a marine "framework" community with topographic relief (i.e., a large structure that stands above the ocean floor). They are constructed by the rapid growth of closely packed, calcareous organisms, and thus the resulting rock type is **biogenic** (biologically produced) limestone. The physical structure of a modern reef itself is nothing more than layer upon layer of abandoned coral skeletons, thus the only living part of the reef is the thin skin of coral animals on the outer surface. Most substantial reef buildups are found in relatively shallow, warm water areas removed from the influence of large rivers, which deliver clay that dilutes the carbonate and clogs the organisms. Because this rock is precipitated in place by the upward growth of coral or other animals, it is not bedded. Instead, the structural details of the reef animals themselves are preserved in a massive framework, and the outline of the original reef can often be seen in the surrounding rock.

Al Fagerstrom (1987), in an effort to better understand reef communities, identified five different guilds that could be traced and compared through time. In his scheme, the resource for which organisms are competing is <u>space</u>. His groupings are as follows, with examples given from modern reef communities:

1. **<u>Constructors</u>** - These are the organisms that build the actual framework structure of the reef. When you visit tropical reefs today, the big coral heads you see first are the constructors: massively calcifying, scleractinian corals.

2. **<u>Bafflers</u>** - The chief role of the bafflers is to block or slow the flow of water over the reef and cause the deposition and stabilization of loose grains. These animals usually wave back and forth in the current on stalks attached to the constructors below. Because of their delicate, fan-like nature, bafflers are often not preserved as intact, whole organism fossils, but rather as broken pieces in the surrounding sediment. Common examples are the sea fans, colonial animals in the same class as corals.

3. **<u>Binders</u>** - This is the glue that holds it all together. These organisms are encrusters that often exhibit rapid lateral growth as they cover surfaces and fill the interstices of the reef. Members include sponges (which may also be members of the constructor guild) and calcifying algae.

4. **<u>Dwellers</u>** - Animals that live on or in the reef simply because they prefer a hard substrate are the dwellers. This is a diverse assemblage of solitary, mobile or sessile organisms (e.g., sea anemones, gastropods, crustaceans, fish, echinoderms, brachiopods, etc.).

5. **<u>Destroyers</u>** - These are animals that bore into, bite off, or otherwise destroy the structure of the reef. These include solitary, mobile animals like parrotfish, sea urchins, and starfish that prey on the coral polyps, and also again include some types of sponges that bore into the reef. The end result of the actions of destroyers is copious fine carbonate mud, which fills in the crevices of the reef or is transported to nearby environments.

As you read about and examine the reef material from different time periods, try to imagine which of the guilds various animals belong to. Some will be much more obvious than others will. Visualize the animals as they were when alive, and think about how they may have related to each other spatially. This is all part of reconstructing ancient environments and communities.

Paleozoic

Paleozoic reef assemblages are very different from the modern scleractinian reefs we are used to. Organisms making up these reefs not only belong to different classes and orders, but even different phyla or kingdoms from the reefs of today. Note, however, that although the organisms are completely different, the guilds identified in modern reefs are present, for the most part, in their ancient counterparts.

Up until the Cambrian Period, most biogenic structures existing in the world were stromatolites, mounds of laminated sediment constructed by photosynthetic bacteria. With the "Cambrian Explosion" and the diversification of calcium carbonate skeletons, reef buildups became more abundant and complex. The first animals to construct what could be considered true reefs were the archaeocyathids. Archaeocyath reefs existed for a short time in the Cambrian. These were replaced by the typical Paleozoic reef assemblage in the Ordovician, which then persisted for much of the era. Contrary to later communities, constructors did not dominate in the earliest reefs. Instead, binders and bafflers were the prevalent organisms. Bryozoans and sponge-like organisms called stromatoporoids were abundant as binders, while bafflers included the stalked crinoids and branching or fan-like bryozoans. Scattered colonial tabulate and rugose corals also characterize the Paleozoic reefs. These, along with calcareous algae, were the constructors, which played a subordinate role in the reef ecosystem compared to today. The dweller guild was the most diverse (as it is today), and included many now-extinct members of the molluscs, brachiopods, and trilobites. Fossil evidence for destroyers is scarce, another sharp contrast with modern reefs.

An interesting endnote to Paleozoic reef assemblages is provided by the Permian "Glass Mountains" fauna, an exquisitely preserved, silicified reef from Texas. The most unusual forms in this assemblage were large, cemented, cup like brachiopods that played the role of constructors. Other dominant organisms were calcareous green algae, sponges, and a dazzling array of molluscs and brachiopods. Bryozoans and crinoids were present but less important than in other Paleozoic reefs. We have provided several examples of the brachiopods that have had the carbonate matrix dissolved away so you can see them. Please be very careful with them! They are essentially "made of glass".

Mesozoic

The close of the Paleozoic brought the extinction of nearly all the rugose and tabulate corals and most of the brachiopods, crinoids, and bryozoans. As such, Mesozoic reef assemblages were very different in nature. Scleractinian corals arose in the Late Triassic; thus corals and sponges characterized many of the Mesozoic reefs. During the Cretaceous, however, a bizarre type of bivalve appeared that completely dominated the environments in which reefs usually developed. These were the **rudists**. The rudists originated in the Jurassic as a small group of slightly aberrant reef dwelling bivalves. By the end of the Cretaceous, however, there were over 100 genera of rudists. In some of the rudists, one valve became long, cone-shaped, and massively calcified, while the other was reduced to form a cap-like lid. Although not truly colonial, these conical molluscs grew upright and packed together, some reaching heights of a meter and a half! Other rudists grew both their valves into fantastic, coiled shapes resembling a set of buffalo horns!

Rudists are very poorly understood creatures. In fact, it is still an area of active debate among rudist workers as to whether or not rudist assemblages should actually be considered reefs. Rudist assemblages are atypical of most other reefs in part because they exhibit a paucity of dwelling and binding organisms. It is possible that the absence of the ammonites, brachiopods, and echinoids indicates a more fluctuating physical environment (temperature, salinity, and oxygen) than these dwellers could tolerate. Other researchers suggest that flourishing growth of the rudists choked out other organisms that could potentially have lived with them. Scleractinian corals, not yet large or diverse, filled the scant baffler guild. Evidence for destroyers is present in rudist reefs mostly in the form of boring sponges (and that doesn't mean dull and uninteresting!), echinoids, and boring "lithophagid" bivalves.

Cenozoic

A wealth of information is available about the more modern, scleractinian coral reefs because they can be easily observed today. Cenozoic reefs have reached the zenith of calcification, growing at fantastic rates. The photosynthetic action of algal symbionts in the coral tissue is responsible for this ability to deposit massive amounts of carbonate. A major question in paleobiology is whether or not the main constructors of fossil reefs also contained such symbionts. The best potential so far seems to lie with the rudists, for their massive buildups are difficult to account for with normal bivalve growth rates.

Guild membership in modern reefs was touched upon in the discussion of Fagerstrom's paper, so we will not repeat it here. We have provided samples from both modern and fossil reefs for you to compare. The fossil material is from the 125,000-year-old Key Largo Limestone, which makes up much of the Florida Keys. See if you can identify some of the modern corals in the Key Largo limestone. Are there any other organisms present besides the coral? What are the spaces between corals filled with? How do these samples differ from older ones? A spectacular exposure of this unit occurs on Big Pine Key, where huge coral heads are clearly visible in a quarry wall. Some heads had evidently been tipped over during large storms, and some show evidence of regrowth in the new upward direction. Smaller corals, binding calcareous algae, numerous dwellers, and abundant destroyers are also present in the rock.

TERRESTRIAL ASSEMBLAGES THROUGH TIME

Terrestrial assemblages are more difficult to discuss in a coherent ecological framework because there are so many different subenvironments within the terrestrial realm. In lieu of this, we will instead summarize some of the major innovations acquired during the evolution of land-based organisms, both plant and animal. You should also keep in mind that the fossil record of terrestrial organisms is far less complete than that for marine (remember the marine bias discussed in Lab 2); therefore, evolutionary relationships among animals are often sketchy and unclear.

Paleozoic

Prior to the appearance of the first land plants in the Silurian, the terrestrial world was not completely barren, but inhabited by a diverse suite of microbial organisms. Some were photosynthetic, others heterotrophic (eating other microbes), and all contributed to the development of very ancient soils preserved in the rock record. The first steps toward a terrestrial existence by multicellular life were taken by the green algae and several groups of specialized fish and arthropods.

The subsequent story of terrestrial life during much of the Paleozoic is one of invasion, diversification, and evolution, rather than extinction, with some organisms becoming progressively better adapted to life out of the water.

The first land plants were small, simple, diminutive plants that colonized the muddy fringes of coastal swamps. The main innovation that led to their further diversification and success was the appearance of a vascular system -- a network of minute vessels that carry water, nutrients, and the products of photosynthesis throughout the plant. This system allowed plants to become more complex during the Devonian by evolving specialized parts for different functions: leaves for photosynthesis, stems for structure and rigidity, and roots for the absorption of water and nutrients. Though the earliest land plants were quite simple, they changed the surface of the earth considerably by accelerating the formation of soils and anchoring those soil particles in place.

The colonization of land by plants was probably the key to subsequent colonization by animals. Some of the earliest land animals were arthropods that lived within the shelter of plants. The majority of these arthropods were probably carnivorous on other invertebrates, but others may have fed on the plant remains, algae, and decomposing fungi. In any case, we know that the first insects lived in close association with swamp plants since their remains are often found fossilized together. Though soft-bodied invertebrates are missing from the fossil record, it is likely that they too were present in late Silurian/early Devonian swamps. By the end of the Devonian, plants had evolved leaves, roots, and wood. Many of the plant groups whose modern representatives are small and insignificant grew to giant proportions during this time. Trees like Lepidodendron - related to the tiny ground pines of today, Calmites - related to modern horsetails, and tree ferns flourished. (Look for the specimens provided of parts of these common fossil plants). The first seed plants also appeared during the Devonian. The seed is important for plants because it (1) provides a protective capsule for the plant embryo and (2) houses a rich food supply to nourish the young plant as it grows its first roots and leaves. These early seed plants gave rise to lineages important in the Paleozoic (seed ferns), Mesozoic (conifers and cycads), and today (flowering plants). Other than ferns, which produce spores, most of the plants you are familiar with are seed plants.

Meanwhile, the arthropods continued to diversify, both taxonomically (137 genera collected at 1 site!) and ecologically. By the end of the Devonian, insects had evolved wings, which facilitated dispersal, feeding, radiation into new habitats, and led to some jumbo-jets of the arthropod world. Carboniferous dragonflies reached lengths of 60 cm! Other large arthropods such as spiders and centipedes were important predators, evolving new hunting tactics like webs, while still others specialized to feed on leaves, sap, roots, or stems. Other than the arthropods, the only other invertebrate groups to successfully invade the terrestrial realm were assorted "worms" and the gastropod molluscs. Even today, out of more than 30 invertebrate phyla, these are the only groups represented on land.

The transition between the Devonian and the Carboniferous also saw the earliest terrestrial vertebrates: the lobe-finned fishes (e.g., lungfish). These were soon followed by early amphibians like Ichthyostega. Although amphibians live a more or less terrestrial life, they still need to return to water to lay their eggs. From the end of the Carboniferous to the middle of the Permian, carnivorous amphibians topped the food chain, feeding on fish, land invertebrates, smaller amphibians, and probably the first reptiles.

The advent of a shelled egg was to the vertebrates what the seed was to plants. Eggs with shells appeared with the first reptiles during the Pennsylvanian. Some of the oldest reptiles are lizards found preserved inside the upright, once-hollow stumps of giant trees from Nova Scotia. The most famous Paleozoic reptiles are the pelycosaurs, sailed reptiles like Dimetrodon that appear in cereal-box dinosaur collections but which are actually more closely related to mammals.

The end of the Paleozoic was marked by climatic cooling and drying as deserts spread across continental interiors, glaciers advanced from the poles, and the steamy Carboniferous swamps dried up. These changes led to the extinction of many Paleozoic organisms, but seed plants and "mammal-like reptiles" survived to provide the stem lineages for subsequent radiations.

Mesozoic

Early Mesozoic forests were dominated by gymnosperm plants such as conifers and cycads. Many familiar conifers like Ginkgo, cedars, and junipers appeared and diversified tremendously in the Jurassic. Ferns continued to be an important component of the ground cover, but the tree ferns of the Paleozoic had for the most part become extinct. Some ferns even adapted to the dry conditions and spread in great, savannah-like "grasslands", creating new habitat for large animals.

The reptiles were the first truly terrestrial animals that did not depend on an aquatic environment for reproduction, allowing them to attain great diversity in both form and ecology. Adaptations such as drought-resistant eggs, evaporation-reducing skin and internal fertilization allowed the reptiles to radiate into arid habitats where no previous chordates could have survived. Species ranged from forests to open landscapes to deserts. Some returned to the sea, such as the plesiosaurs and ichthyosaurs, while the pterosaurs (flying reptiles) took to the air. Some were carnivores; others ate plants, or were scavengers. Though some dinosaurs and other large reptiles grew to enormous proportions, most early reptiles were smaller. Recent work has shown that the dinosaurs were more active and dynamic than previously thought, perhaps even being warm blooded. Evidence has shown that some dinosaurs traveled in herds and migrated, and others laid their eggs together in "nursery" communities and cared for their young after hatching.

Though reptile-like mammals such as therapsids had been around since the late Carboniferous (predating the dinosaurs), the first true mammals didn't appear until early in the Mesozoic. Since almost every terrestrial Mesozoic niche was dominated by the dinosaurs, the mammals stayed small and insignificant until the extinction of the dinosaurs at the end of the era. The first birds also appeared in the Mesozoic from one of the two major lineages of dinosaurs, indicated by the famous Jurassic fossil of Archaeopteryx. Small amphibians, turtles, and crocodilians flourished during this period as well.

The major transition from Mesozoic to Cenozoic type plants took place in the mid-Cretaceous with the evolution of flowers, which are specialized reproductive organs. The first angiosperms (flowering plants) were restricted in their distribution and were slow to diversify, but once forms appeared that could inhabit forested areas an explosive radiation ensued. This radiation coincided with an explosion in insect diversity: the bees, wasps, ants, butterflies, and moths (important pollinators) also first appear in the Cretaceous. The subsequent diversification of insects and angiosperms is thought to have occurred by co-evolution: the highly specific, synergistic relationships that evolved between particular species of plants and insects. Eventually, the angiosperms displaced conifers as the dominant trees in most low-latitude forests, which is a position they retain today.

Cenozoic

The extinction events that marked the end of the Mesozoic and the Age of Dinosaurs was not felt markedly by terrestrial plant communities. Angiosperms (and insects) continued to radiate, with the loss of only a few groups at the boundary. Important new additions were the grasses, well adapted to thrive in the cool, dry interiors of continents. The expansive grasslands present today are thus a relatively recent phenomenon, but they have played pivotal roles in the evolution of many large mammals, including us.

The Cretaceous/Tertiary boundary was a crucial turning point for terrestrial vertebrates. The giant impact event and ensuing devastation that defines the boundary (see Alvarez et al., 1980, in your sourcebook) caused the demise of the dinosaurs and permitted the radiation of mammals, which until this time had been hiding in the nooks and crannies of the dinosaurs' world. (As you ponder the contingent nature of life's history, consider what the world might be like today had that asteroid not fallen and prematurely snuffed out the reign of the dinosaurs.) The entire range of Cenozoic mammals evolved from small, shrew-like ancestors, producing forms that filled roles previously occupied by dinosaurs. The Eocene and Pliocene were times of particularly large size for mammals, with huge relatives of elephants, cows, rhinos, deer, armadillos, and sloths that were hunted by giant cats, dogs, and bears. Though the first primates originated in the Cretaceous before the major diversification of mammals, a side branch of the primate lineage adopted an upright posture during the Pliocene and moved from the forest into the grasslands. Descendants of some of these primates would persist through the Pleistocene Ice Age and go on to affect the natural world in a more significant way than any other animal.