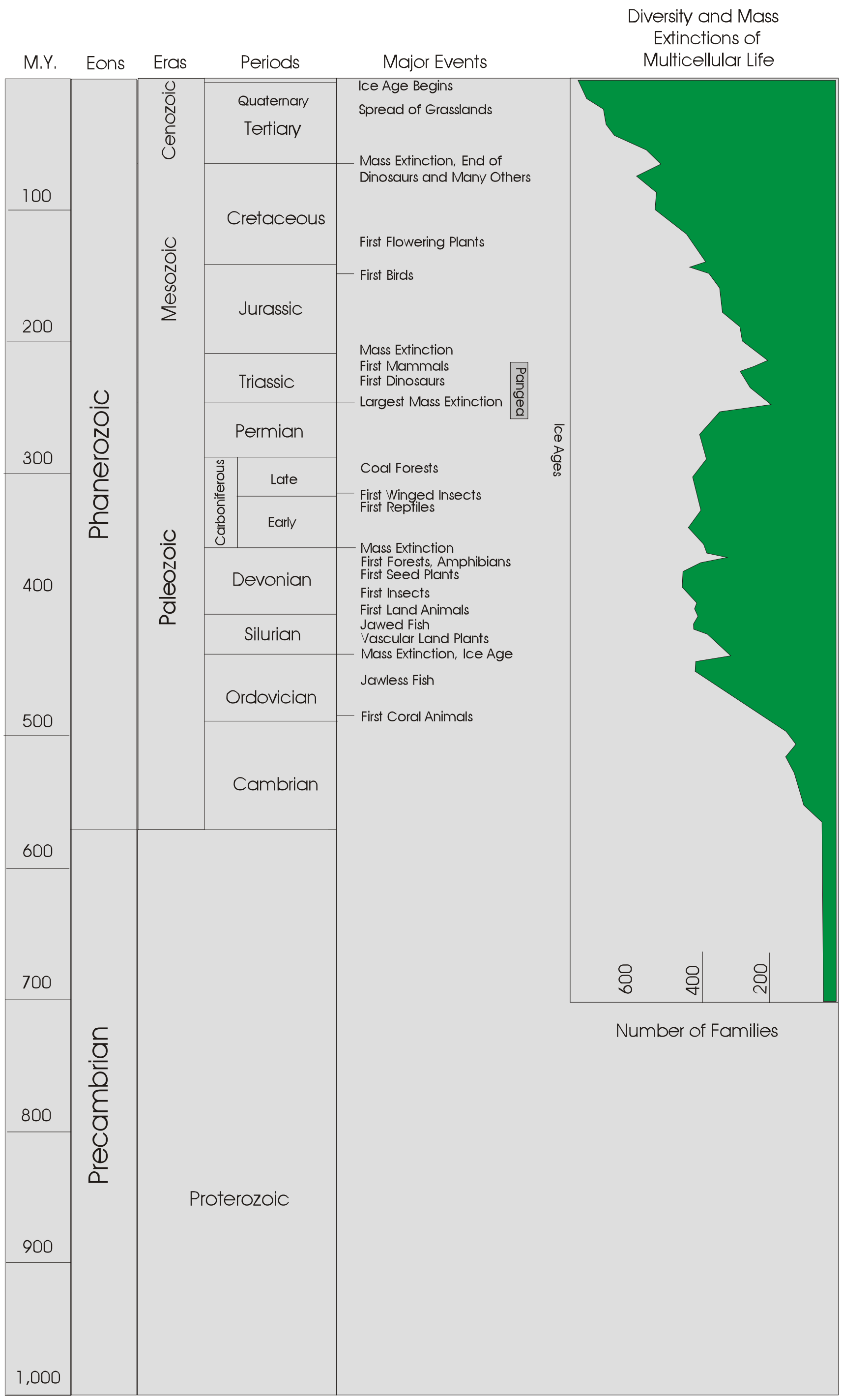
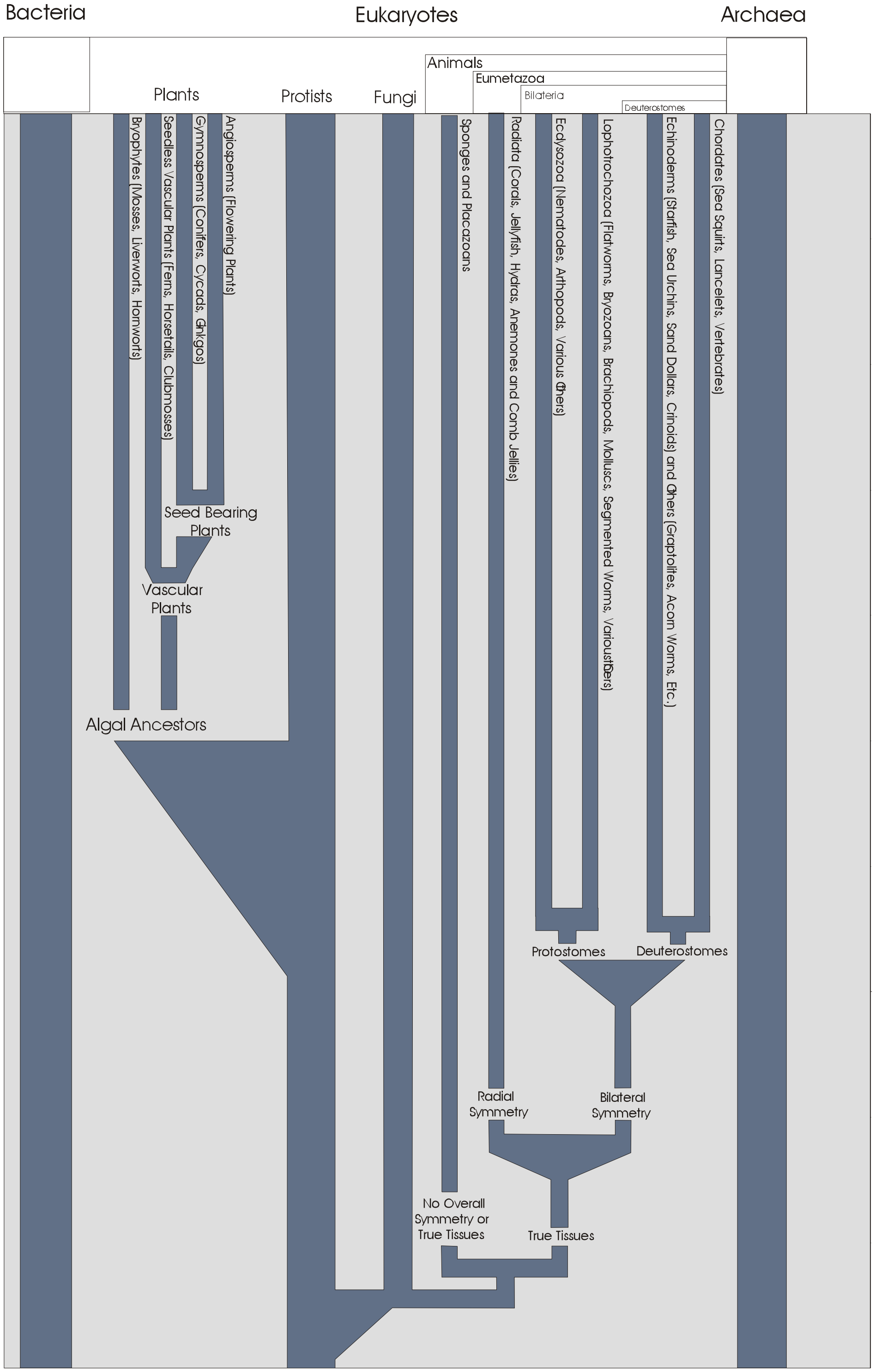
RECENT LIFE

Note to Online Readers: This chapter still needs some work. I still need to write the section on dinosaurs, and I need to update chordate phylogeny, and probably animal phylogeny, which seems to have been re-constructed recently. When I get permission, I will include maps of the distribution of continents at various times.

The Evolution of Multicellular Life



Emphasizing Plants and Animals



LIVING LARGE: MULTICELLULAR LIFE

This chapter is entitled "Recent Life", because most multicellular life really is quite recent compared to single-celled organisms. But the key word here is relative. By our standards, multicellular life has been around for quite a long time. The first multicellular organism known is a kind of algae that dates back 2.2 billion years. By 1 billion years ago there were several types of simple multicellular algae. Algae and the cyanobacteria would provide the photosynthetic foundation of the biosphere for hundreds of millions of years. Plants would join them about 500 million years ago; becoming the basis for life on land. Even today the older algae and cyanobacteria are the basis of most marine ecosystems. If we were going to be truly unbiased, then, we would delve more deeply into the ways of algae, and the way multicellular algae arose. But we are land creatures, who encounter plants, animals, and to a lesser extent, fungi, far more than algae. So, let's be a bit more provincial, and zoom in from the amazing variety of lifestyles represented by the prokaryotes and protists, to the more familiar, and visible, large organisms. Figure .1 is the timeline plotting the major events and trends in this part of our story.

FUNGI

The three kingdoms of multicellular life we encounter most here on land are plants, animals, and fungi. Fungi, such as yeasts, many molds, and mushrooms, are the least familiar to the layperson. They are often lumped with plants, because both are sedentary and lack nervous systems. But a fungus is very different than a plant. Like plants, they have cell walls, but their cell walls are made of chitin, not cellulose. Unlike plants, fungi are not photosynthetic. They are heterotrophs that get their nutrition from absorbing organic molecules. Some, like many mushrooms on leafy forest floors, live amongst non-living organic matter, plying their unglamourous but vital trade as decomposers. (A mushroom is really just the reproductive organ of a network-like fungus spread out beneath the surface.) Other fungi are parasites, living on or inside other organisms. Some examples are the athlete's foot fungus and the misnamed "ringworm" fungus. Some mushrooms growing around the bases of trees are parasites, while others are more like partners, helping the roots absorb nutrients in exchange for other nutrients from the plant. As many as 95% of plants have symbiotic fungi around their roots, and most would die without them.

Fungi are often considered more primitive than plants, and plants more primitive than animals. But this is another misconception. Plants actually evolved much more recently than the other two groups. Strangely enough, fungi are much more closely related to animals than to plants--fungi and animals seem to have evolved from a common ancestor. We are more closely related to mushrooms and molds than to ferns and oak trees.

THE ANIMAL FAMILY TREE

Jokes about "fun guys" notwithstanding, it's a bit hard to identify with fungi, even if they are our relatives. We are animals, so naturally most of us find animals more interesting. But even animals are the subject of grave misunderstandings. One concerns what constitutes an animal. Some people think only mammals–hairy, warm-blooded creatures that nurse their young–are animals. Others include all vertebrates–fish, amphibians, reptiles, birds, and mammals–but leave out things like insects, jellyfish, worms, and sponges; all of which are animals. Well then, what exactly is an animal? Animals are distinguished by several characteristics. For one thing, they do not have cell walls, as many organisms do. Animals tend to be *motile*–they can move around. They are heterotrophs which have to consume other organisms. Animals are multicellular–they are whole systems composed of many cells working together. Oftentimes, these cells take different forms, to fill different roles. In other words, there is a division of labor among animal cells. In many animals, specialized cells combine into specialized **tissues**, such as connective tissue or nervous tissue. In contrast to plants and fungi, only the diploid stage of the animal life cycle is multicellular. Most animals have small sperm with flagella, which propel them to a larger, stationary egg. These gametes combine to form a zygote that grows and develops through cell division into an adult animal. During this process, the cells arrange themselves into a hollow ball called a blastula. This is a crucial distinction between animals and other groups. In fact, the major groups of animals are distinguished by what happens later in development, as we will see.

As would be expected from all their common features, all animals seem to be descended from a common ancestor. This ancestor probably resembled a type of protist called a choanoflagellate, a flagellated organism that groups together into colonies of identical cells. These colonies don't have specialized cells, so they don't technically constitute multicellular organisms. At some point the early colonial organisms from which animals are descended began to differentiate internally, so that different cells began to take different forms and serve different purposes. Gradually, the cells became expendable parts of the larger organism, which maintained itself as cells came and went. Like other multicellular organisms, animals represent a new level of organization, a higher-level aggregation of parts into a unified whole.

Now, the question here is this: why did the cells "allow themselves" to become expendable parts, many of which die on cue or never reproduce? What sense does such behavior make if evolution has created organisms that tend to try to stay alive long enough to reproduce successfully? It only makes sense because every cell in the multicellular organism has identical genes. They all have the same biological interests. It is fine for a cell to die without reproducing, as long as other cells with identical genes do reproduce. So, most of the cells give up their reproduction functions, in order to help the organism as a whole to survive and reproduce. Copies of genes straight from their own DNA won't make it into future generations, but that is fine, because copies of identical genes will.

This highlights an important point. Cells didn't aggregate into multicellular organisms because it was the next step in the march toward complexity and interconnectedness. They did so because it happened to be evolutionarily advantageous–the combined cells had a higher reproductive fitness than separate ones. Evolution does not select for complexity for its own sake, and the vast majority of organisms on Earth today are still unicellular. But if complexity happens to be useful, it will be retained. Multicellularity might have been useful for any number of reasons. One is that multicellular organisms have niches available to them that unicellular organisms do not. Simply being larger can be advantageous–a plant can grow toward the light in a way that a single cell, or even a colony, could not. Specialization of cells and tissues can be especially advantageous. A single-celled organism has to compromise between several functions, such as reproduction, feeding, and locomotion. A multicellular organism can let various cells specialize completely, which lets them do their jobs more efficiently. So, while multicellularity never caught on for most organisms, it proved quite useful for a few.

Now, you may have noticed an apparent paradox. If every cell in a multicellular organism is genetically identical, and genes control how the cell develops and runs, how can cells take on different forms and serve different roles? The answer is that the genome contains the instructions for every type of cell in an organism. The human body, for example has over 200 different kinds of specialized cell, but they each have the same genome. What allows them to differentiate is that some genes are active, and some are not, depending on the cell. My nerve cells have the same set of genes as my liver cells, but the sets of genes *in use* in each one is very different.

But these considerations apply to any complex, multicellular organism. Let's get back to animals. As Figure .1 shows, the basic divisions of animals arose between about 1 billion and 600 million years ago, and they are all based on variations in body plan that arise early in the embryo's development. The oldest branch is the one between sponges and all other animals. Sponges are among the simplest of animals, and they are thought to resemble the first animals. They have no true tissue specialization and only a handful of cell types. While most animals are either radially symmetric, like a starfish, or bilaterally symmetric, like a lizard, sponges have no overall symmetry. They are shaped like a cup, or more commonly, a branching tree of cups. Water flows in through pores in the walls of the cup (driven by the beating flagella of cells almost exactly like ancestral choanocytes), and then out through the opening at the top. Particles of food are filtered from the water as it passes through.

All other animals beside sponges have true tissues, but they differ greatly in their basic body plan. These differences begin early in development. As I mentioned earlier, a defining feature of animals is that the dividing cells of the zygote arrange themselves into a hollow ball called a **blastula**. The blastula then folds inward on itself to form a **gastrula** (Figure .2 **Awaiting permission for image**) The cells lining the inner cavity form a tissue called **endoderm**, and the cells on the outside form the **ectoderm**. In many animals, these tissues go on dividing and differentiating, with the endoderm differentiating into one set of tissues, and the ectoderm into another.

One of the most ancient groups of animals, called the Radiata, has a body plan that is basically a gastrula, often with tentacles around the rim of the opening. This is the basic form of sea anemones, jellyfish, hydras, and corals. Food comes in the opening, and is digested in the central cavity. Wastes go out the way they came in. When these animals anchor themselves to a surface underwater, with their mouth pointing upward, as in sea anemones, they are called *polyps*.

When they float freely, with the mouth facing downward, like jellyfish, they are called *medusae*. Some animals in this group go through a polyp and a medusa stage at different points in their life cycle, while others stick with one or the other.

Radiata are named for their radial symmetry. Animals on the opposite side of this division are called Bilateria, because they are bilaterally symmetric. Bilateral animals have a third layer of tissue between the endoderm and the ectoderm, called the **mesoderm**. The rest of the big divisions among the animals depend on the shape of the mesoderm, and whether it encloses a cavity, called a **coelom** (Figure .3 **Awaiting Permissio for image**). The simplest bilateral animals have no coelom, so they are called **acoelomates**. All acoelomates are types of flatworms, from the tiny planaria in ponds to notorious parasites like tapeworms and liver flukes. A flatworm has an elongated, bilaterally symmetric body. Its digestive cavity, which has only one opening, is surrounded concentrically by endoderm, mesoderm, and then ectoderm, which forms the outermost layer. Unlike anemones and jellyfish, flatworms can be said to have a front end and a back end–a head and a tail. They have concentrations of nerves in the head called *ganglia*; distant forerunners of brains.

The next branches of animals are called coelomates, because they do have a coelom–a fluid-filled cavity that separates their digestive tract from their outer tissues. This separation is useful, because it protects the digestive tract (and the inner organs that develop from the endoderm) from minor bumps to the outer surface. It also disconnects these inner and outer systems, so movement does not unduly disrupt digestion, and vice versa. **Pseudocoelomates**, which include nematodes (roundworms), and tiny, elegant creatures called rotifers, are so called because they don't have a true coelom. The coelomates do have a true coelom, which is enclosed entirely by the mesoderm.

Coelomates come in two major varieties, called **protostomes** and **deuterostomes**. Protostomes include molluscs (such as snails, clams, and squid); annelids (segmented worms); and arthropods. Arthropods are a vast and successful group. In the sea, most arthropods, such as crabs, shrimp, and lobsters; are crustaceans. Pillbugs (also known as sowbugs or roly-polies) are among the few terrestrial crustaceans. Another group of aquatic arthropods, the trilobites, are now extinct. Terrestrial arthropods include centipedes, scorpions, spiders, and most of all, insects. Deuterostomes include echinoderms (creatures like starfish and sea lillies, which have returned to a radial body plan) and chordates, which includes lancelets, sea squirts, and vertebrates such as ourselves.

Both protostomes and deuterostomes have coeloms, but they seem to have evolved separately in each group, which shows how useful it must be to have one. In fact, the differences between these two groups are quite profound. In protostomes, the original opening in the gastrula becomes a mouth, and another opening forms at the other end of the digestive tract, to form an anus. In deuterostomes it is just the reverse–the original opening becomes the anus, and the mouth develops later. Not only that, but whereas we deuterostomes have our central nerve cord behind our digestive tract (toward our back), proterostomes have it in front. Each group is both upside down and backwards compared to the other.

Now, I have been speaking of these divisions in terms of animals that are familiar today. But this is a bit misleading, because these major divisions first separated hundreds of millions of years ago, and the first members of each group were often very different than their descendants. In fact, we don't know much about what the first animals looked like, because fossil evidence from that time is terribly scarce. The main branches have been inferred mostly from comparing more recent organisms, and from molecular genetic technology, because by the time the fossil record becomes clear, the main branches had already been established. The more recent, clear fossil record is the basis of the next part of our story.

NEWCOMERS: LIFE IN THE PHANEROZOIC EON

In the 19th century, when geology, paleontology, and evolutionary biology were being born, life was believed to have begun rather suddenly. Since sedimentary rocks, and the fossils that they contain, are laid down on top of one another as the eons go by, you can look farther back in time by finding places where deeper layers are exposed. Scientists in Wales eventually found a set of rocks that seemed to be the bottommost layer containing fossils. These rocks were full of fossils, but those below them seemed to have no fossils at all. It was as though life had simply burst into existence. The geological period from which these last fossil-bearing rocks date was named the Cambrian Period, after the Cambrian mountains of Wales. Rocks below the Cambrian were labeled Precambrian. Today, we know that the oldest Cambrian rocks are about

545 million years old. Of course, we also know that life began long before that. But the Cambrian is special nonetheless, because it really marks the first appearance of abundant, multicellular fossils. Ancient animals seem to have exploded in diversity at that time, in an event which has come to be called the **Cambrian explosion**.

Actually, the Cambrian explosion may be partly an illusion. Animals from this time had evolved hard shells of calcium carbonate, silica, or other materials. This may mean that these materials first became common in sea water at that time (life was still entirely aquatic then). But the diversity of shell materials suggests that life had simply gotten tougher–many animals had become predators, and the shells were a means of protection. If animals before the Cambrian had soft bodies, they would have left far fewer fossils. In fact, some fossil communities from Precambrian times have been found, and they do tend to be soft-bodied. We know that most of the major animal lineages were established before the Cambrian, so it was not the beginning of animal diversity. Still, a real threshold seems to have been crossed. Animals of the Cambrian seem to be very different, and more diverse, than those before. Scientists are still debating about why that might be, but whatever the reasons, the Cambrian inaugurates a new chapter in the earth's history.

The Cambrian Period marks the transition from the Precambrian Eon to the Phanerozoic Eon (Phanerozoic means "visible life"). The Phanerozoic is divided into three **eras**–the **Paleozoic**, the **Mesozoic**, and the **Cenozoic** (Figure .1). These, in turn, are divided into **periods**, with names most people recognize; such as the Cambrian, Jurassic, and Cretaceous. Even though the Phanerozoic eon accounts for only 12% of the Earth's history, it is by far the most familiar, because its traces have not yet been obscured so much by the passage of time, and because it saw the rise of large organisms that leave better fossils and spark more popular interest than bacteria. It is the source of most of the popular images of prehistoric time; the colonization of land, the rise and fall of the dinosaurs, the fern and cycad forests, and the ice ages. Let's take a deeper look at this eventful stretch of time.

ANCIENT HISTORY: THE PALEOZOIC

THE CAMBRIAN EXPLOSION

At the beginning of the Cambrian Period, the globe was a very different place than today (Figure .3 **Awaiting permission for image**). Lands that would one day form parts of Asia, Africa, Australia, Antarctica, and South America were combined in an enormous southern continent now called Gondwana. A smaller continent, called Laurentia, would one day form the ancient center of North America. Smaller continents would eventually become parts of Europe, Siberia, and Northern China. All these lands were barren wastes; entirely absent of multicellular life.

In the shallow seas above the continental shelves, however, life was teeming. Soft-bodied, multicellular animals had existed for some time, and sizeable mats of bacteria for even longer. With the dawn of the Cambrian, life began to encase itself in hard shells, many of which would be preserved for us to ponder. There were sponges with spiky, glassy skeletons of silica; molluscs with calcium carbonate shells; brachiopods that looked like clams on stalks (though they are not related); and early arthropods with their chitinous outer skeletons. Even some of the bacterial colonies had become hardened with calcium. All this hard material probably evolved as armor against predators, but organisms soon discovered that it was good for other uses, especially as structural support for growing tall, chewing and grasping, and moving about.

Like aquatic communities today, Cambrian communities were based on photosynthetic bacteria and algae (plants would not evolve for quite some time, and they are mostly terrestrial). These photosynthetic producers were fed upon by primary consumers such as sponges, brachiopods, and crinoids. Crinoids, which are sometimes called sea lilies, are relatives of starfish, but they stand on a stalk, which makes them superficially resemble plants. The primary consumers were eaten by secondary consumers such as trilobites and burrowing worms. These, in their turn, were eaten by the top predators; large arthropods and bizarre creatures called anomalocarids, some a half-meter long. These predators kept the populations of primary consumers trimmed back, allowing large reefs of sponges and cyanobacterial colonies to grow. Only later would the reef-building niche come to be filled by true coral animals. Even the top predators were fed upon while still alive by parasites, and everything was eventually broken down and recycled by decomposers.

ZOOMING IN: CHORDATES AND VERTEBRATES

One of the creatures swimming through Cambrian waters was *Pikaia*, one of the earliest known chordates. The chordates are the group that includes the vertebrates, so this is our closest known Cambrian relative. The appearance of pikaia is a good opportunity to start discussing how we fit into the rest of the animal kingdom, by tracing the evolution of the various groups of vertebrates from ancestral chordates. Discuss bias, etc

Fossils of pikaia don't reveal much about its internal anatomy, but they resembled modern creatures called lancelets (sometimes called amphioxous), so we can make a good guess by looking at lancelets. Lancelets, as their name suggests, are blade-shaped animals, which have no cranium, fins, jaws, or eyes. Like the ancient chordates they resemble, they are rather featureless creatures, but they do have all four essential features of a chordate–a hollow, dorsal nerve chord, a **notochord**, pharygeal (gill) slits, and a muscular tail extending past the anus. Now, you may be examining yourself and finding that you do not have all of these features. Not to worry. You did as an embryo. Many chordates only possess all four features during embryonic development.

The chordate nerve chord is unusual in that it runs along the back, or **dorsal** side, instead of the belly, or **ventral,** side. This nerve chord develops from a hollow tube, and even humans have a tiny cavity in the middle of their spinal chord. If you watch an earthworm or other animal without any hard scaffolding, you will notice that it tends to compress and expand like an accordion. This is prevented in Chordates by a stiff, but flexible, rod called a **notochord**, which lies just underneath the spinal cord. The notochord keeps the body from compressing, and serves as an attachment for rows of muscles which bend the notochord back and forth, allowing the animal to swim efficiently.[1] In vertebrates, the notochord is present only in embryos, and it later becomes the discs between the vertebrae. Another feature present in ancestral, primitive, and embryonic chordates is a set of pharyngeal slits. The word *pharyngeal* refers to the **pharynx**–the space constituting the back of the mouth. These slits probably served as sieves to filter food particles from the water in the earliest chordates, as they still do in lancelets. Later, they became gill slits, allowing early vertebrates to extract oxygen by passing it over their gills and out through

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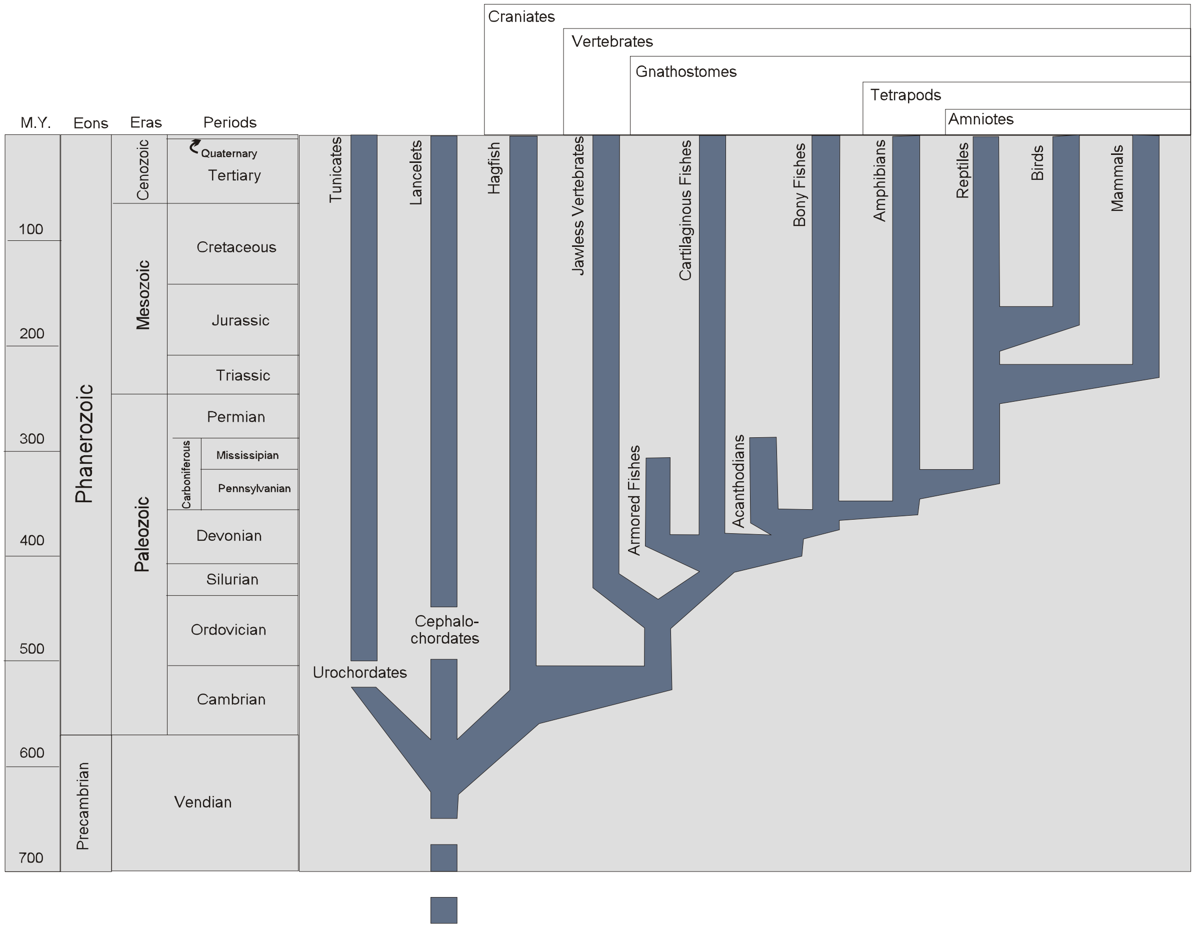
[1] Today's lancelets spend most of their time burrowed tail-first in the sand, filtering out drifting particles, but they are quite capable of swimming when they need to. Pikaia probably spent most of its time swimming, since predators fierce enough to drive it underground had not yet appeared.

Figure .4 Simplified Evolutionary History of Chordates, Emphasizing Vertebrates



the slits, instead of absorbing it through their skin. In humans, pharangeal slits are only present when we are embryos. Barring developmental abnormalities, the same is true for the fourth characteristic of chordates–a muscular, postanal tail.

As Figure .4 shows, the phylum chordata is divided into three subphyla--*Urochordata*, *Cephalochordata*, and *Vertebrata*. **-hemichordates-** We have already met the only modern cephalochordates–the lancelets. Urochordates resemble lancelets as embryos, but they change drastically as they mature, becoming stationary animals commonly called tunicates, or sea squirts. These creatures siphon water in through one opening, filter out food particles with their pharyngeal slits, and eject the water out of another opening. They can eject it quite forcibly if bothered, which is why they are called sea squirts.

The third subphylum is our own–the vertebrates. Obviously, a defining characteristic of vertebrates is the vertebral column, the row of bony or cartilaginous vertebrae that enclose and protect the spinal chord. But there are other defining features. A deeper feature is a structure called the **neural crest**, a set of cells that appears between the nerve cord and the ectoderm during development (Figure .5 **Awaiting permission for image**). These "leftover" cells go on to form other structures, including many bones of the skeleton. The internal skeleton of bone or cartilage is another defining feature of vertebrates, as is a closed circulatory system. Vertebrates tend to be highly *cephalized*, with nervous tissue and sense organs concentrated around the head. In general, vertebrates are adapted to a very active, mobile lifestyle. They tend to go out and find their food; an active approach to life that requires sophisticated sense organs, nervous systems, and means of getting around. In short, they have evolved to fill the "large, complex animal with big brain" niche. The first true vertebrates probably appeared during the Cambrian period, but they didn't become common until later periods, so we will postpone discussing them until then.

THE ORDOVICIAN: AQUATIC INNOVATIONS AND THE FIRST PLANTS

Atmospheric carbon dioxide levels were high as the Ordovician Period began, and a corresponding greenhouse effect kept the Earth relatively warm. Sea levels were also high because there was little ice at the poles. True coral animals evolved at this time, along with lacy, spongelike **bryozoans**, both of which helped build Ordovician reefs. **Cephalopods**; squid-like molluscs with shells, evolved and joined the diversifying trilobites as predators. *Conodonts* were slender, eel-like chordates. These had rows of comb-like teeth, which were preserved as fossils in Ordovician strata.

Perhaps the greatest innovation of the Ordovician left only tiny, fossilized spores as a legacy–these were the first plants. Plants seem to have evolved from multicellular algae. What distinguished them, and all plants today, was that they retained and sheltered fertilized zygotes as they grew into multicellular embryos. As I mentioned in the last chapter, all plants have alternating generations, where both the haploid generation (one set of chromosomes) and the diploid generation (two sets of chromosomes) are multicellular. The first plants resembled **bryophytes**, the group containing modern mosses, hornworts, and liverworts (see Figure .1 for the evolution of major plant groups). They would have reproduced in the same way, so we can use mosses as an example of early plant reproduction.

When you think of a moss–a green plant growing low along damp ground–you are thinking of the haploid generation, which is the dominant generation in bryophytes. This generation produces sperm in a specialized organ called an *antheridium*. The sperm swim through the film of water that usually coats the plant to egg cells, which are sheltered in an organ called an *archegonium*. Once fertilized, the zygote begins to grow into an embryo, still tucked away in the archegonium. This embryo will grow into the multicellular diploid generation. In mosses, these objects are sometimes visible as brownish stalks that sprout out of the haploid greenery. Haploid **spores** are produced in capsules at the tip of these stalks through meiosis. These capsules eventually pop open, releasing the tough, waterproof spores. Those that find a suitable, damp, spot will germinate, growing into another diploid generation.

Their protection of their embryos, and their water resistant spores, allowed the first plants to venture tentatively onto the land, but the need for their sperm to swim restricted them to damp areas close to the water. These first plants, and their descendants–the mosses and their relatives–were non-vascular. That is, they had no internal tubing to carry water and nutrients from place to place. Instead, they had to rely on diffusion through their tissues, which kept them from growing very large. The land had begun to be colonized nonetheless, and patches of green spread just a few paces out of the water; taking the first steps onto the barren continents.

The emergence of plants was just a part of a great radiation of life that occurred during the early Ordovician, as new organisms discovered new niches. Some adopted the **plankton** way of life, as tiny producers and consumers floating in the open ocean. Plankton provided an ecological foundation for higher level consumers to move into the open ocean. Other organisms colonized the deep ocean floors. The party ended for many however, toward the end of the Ordovician. The great continent of Gondwana had moved over the south pole as the world was cooling off. An ice cap began to form, which lowering sea levels, and lead to a cascade of events that cooled the world down further. All these changes resulted in a mass extinction of many groups of organisms, the first major mass extinction of multicellular life.

THE SILURIAN: JAWLESS FISH AND GIANT SEA SCORPIONS

The cold conditions of the late Ordovician didn't last long (as such things go). Over the first 20 million years or so of the Silurian Period, the earth warmed again and sea levels rose. The small continents of Baltica and Avalonia began to collide with Laurentia, raising high mountains that would later become part of the Appalachians of North America and the Caledonian Highlands of Scotland. Strange hemichordates called **graptolites**–drifting colonies of small animals bound together by calcium carbonate shells--also expanded greatly. These now-extinct creatures left numerous fossils which would someday puzzle generations of paleontologists before they finally decided what a living graptolite looked like. As the high seas flooded low-lying continental lands, the warm, even climate encouraged enormous reefs to grow. One great fossil reef lies just under the lower Great Lakes area of North America, stretching from Ontario to Indiana. Plants began to acquire vascular systems, which allowed them to grow up to two meters tall, though they were still confined to damp areas. Among the top predators were the *euryptrids*; close relatives of scorpions which grew up to *3 meters long*. If a more frightening creature ever lived, I have not heard about it. True scorpions and pseudoscorpions, of more reasonable proportions, seem to have been among the first creatures to venture onto the land, leaving fossil footprints as the Silurian drew to a close.

It was during the Silurian that early vertebrates first became common; in the form of large, jawless, armored "fish". The reason for the scare quotes around the word fish is that it is a bit problematic, biologically speaking. Creatures known as fish cover a wide range of groups that are not very closely related. A trout, for example, is as closely related to a frog as it is to a shark. So, the word is fine as a convenient term for certain groups of aquatic vertebrates, but keep in mind that it not technically well-defined. One "fish", the modern-day hagfish, is not even a vertebrate (though it is a chordate)(Figure .4). Nor is it an attractive animal. Because they release astonishing amounts of slime, hagfish are sometimes called slime eels. They are shaped like an eel, but unlike true eels (which are bony fishes) they don't have jaws. Instead, they have a ring-shaped mouth lined with teeth, which they use to eat their way through dead and dying sea creatures. Hagfish don't have a real backbone, so they are not vertebrates. They do have a cranium, however, so they are lumped with vertebrates in a larger group called **craniates**.

The only living jawless vertebrate is an equally unattractive animal called a lamprey. Lampreys look superficially similar to hagfish, with the same kind of radial mouth. They are parasites, which use their suction-cup mouths to attach themselves to, and feed on, living fish. Until recently, lampreys and hagfish, along with the extinct jawless fish, were grouped together as *agnathans*. But it seems that there were actually several lines of jawless vertebrates, all of which are extinct except for the lampreys (the hagfish turned out not to be vertebrates). So, it is better to think of these as primitive, jawless vertebrates, instead of constituting a self-contained group, which they do not. The reason they do not is that some extinct jawless fish were more closely related to the jawed fish than to each other. The first fish with jaws were the first members of a true biological group–the **gnathostomes**, or "jaw mouths". These appeared early in the Silurian period, but they would not expand until the next period, the Devonian.

THE DEVONIAN: LIFE MARCHES ASHORE

The Devonian was an eventful period. The vascular plants grew more widespread, staking claim to more of the land all the time. Since plants are mostly above water, they take carbon dioxide straight from the air (instead of from the water), and replace it with oxygen. By the Devonian, plants had brought oxygen in the air to a level that could support numerous land creatures. The first of these had been scorpions and pseudo-scorpions. These were followed in the Devonian by the first insects, a truly terrestrial group of arthropods that would prove wildly successful in this new environment. As the Devonian went on, the plants spread and grew larger. Spore-bearing vascular plants, such as ferns and clubmosses, were the first to discover a new niche, and became tall enough to be called trees. By the late Devonian, the first real forests were starting to spread across the landscape.

JAWS

The Devonian Period is sometimes called the "Age of Fishes" because the jawed fish began to diversify during this time. Jaws had developed in the Silurian period, from skeletal rods beneath the gill slits. Some of these rods grew larger and became joined by a hinge, thus forming the first simple jaws. The first fish with jaws to appear in the fossil record were armored creatures called **placoderms**. These were soon joined by a group called **acanthodians**. Both of these groups, which are now extinct, had mouths with sharp, bony edges, but no teeth. The two major groups of fish remaining today do have teeth, which may be one reason they are still around. The **Chondrichthyes**, or cartilaginous fish, includes the sharks, skates, and rays. As the name suggests, these fish have skeletons of cartilage, often reinforced with calcified granules. One might assume that cartilaginous skeletons are the primitive condition for fish. But they aren't. The first fish had bony skeletons. Why the sharks and rays replaced bone with cartilage is still an unsolved problem, but it seems to have worked out well for them.

The other great group of fish is the **Osteichthyes**, or bony fishes. Bony fish, needless to say, have bony skeletons. They also have an *operculum*, a flap covering the gills, which can be moved back and forth to draw water through. The operculum lets bony fish breathe easily while motionless, in contrast to cartilaginous fish, who have to constantly swim or laboriously pump water across their gills. The first bony fish seem to have originated in fresh water during the great Devonian radiation of fishes. Their eyes were not much use in the murky water, so they used their sense of smell to find their way around. Like today's fish, they had no ears. Instead, they detected water-borne vibrations with a long line of sensory devices down their side called a *lateral line organ*. Oddly enough, they had simple lungs, which they would fill by gulping fresh air when oxygen became depleted in stagnant pools. The *ray-finned fishes*, named for the rays which support their fanlike fins, moved into ocean water. There lungs were no longer terribly useful, so they were modified into swim bladders. These can be filled with internally generated gases, so the fish can adjust its buoyancy, which allows it to float at various depths.

The other group of bony fishes, the *lobe-finned fish*, kept their lungs. Lobe-finned fish are named for the muscular lobes to which their fins are attached. These allowed the fish to crawl along the bottom of the pools and swamps they inhabited. One type of lobe-finned fish, the lungfish, still exists in stagnant pools in the southern hemisphere, occasionally gulping air as they have done for hundreds of millions of years. Other types of lobe-finned fish are known from the fossil record, but they are mostly extinct. They were thought to be entirely extinct until a fish called a *coelecanth* was pulled up off the coast of Madagascar in 1938. This was a living member of a group thought to have gone extinct 60 million years ago, so biologists were understandably shocked. Since most bony fish today are the ray-finned kind, one might think that they turned out to be more successful than the lobe-finned fish. But that is not exactly true. The descendants of the lobe-finned fish proved to be quite successful. It's just that most of them are not fish anymore.

GROWING LEGS

During the Devonian period, some of the lobe-finned fish were becoming well adapted to life in shallow, stagnant pools. The earliest lobe-finned fish, like other jawed fish, had tubelike nostrils, through which water entered, passed across smell receptors, and then exited through another opening nearby. These nostrils were only for smelling, not breathing. This arrangement was modified in some groups so that the nostril opened into the mouth, just above the front teeth. This allowed the fish to breathe air when needed, simply by raising its nostrils out of the water. The lobed fins helped them push themselves out of the water to take a breath of air, as well as propel themselves along the bottom. Their ribs began to grow heavy, in order to support the lungs against the fish's weight. Some of these fish were probably able to crawl to other ponds when their own dried up, using a swimming motion to catch the ground with their lobes and pull themselves forward.

The first known creatures with four legs appeared by the end of the Devonian period, about 360 million years ago. As figure shows, all modern terrestrial vertebrates are descended from these first four-legged creatures. Consequently, they all belong to the group called **tetrapods**, which means "four legs". Obviously, some creatures such as snakes and birds no longer have four legs, but their ancestors did, so they are still considered tetrapods. The first tetrapods probably spent almost all their time in the water, and limbs may have developed as much to help the animal crawl around in shallow water as to move overland. Once they could move on land, however, the selective pressure would have been strong to develop better legs, because it allowed the owners of those legs to find better pools of water, and to feed on the newly abundant land arthropods, such as scorpions and insects.

Some of the first tetrapods were formidable creatures, resembling a cross between a fish, a salamander, and a crocodile. The first tetrapods were traditionally considered amphibians, like today's frogs, toads, and salamanders. However, many of them were as similar to fish as to modern amphibians, and many paleontologists refer to them as *stem-tetrapods*, reserving the term *amphibians* for later animals, many of which were also quite large. For convenience, I will refer to all of the first tetrapods as amphibians. In any case, long before we were around to quibble about their classification, these creatures did quite well, becoming the dominant terrestrial vertebrates for a few million years after the Devonian.

During the late Devonian, the climate was cooling, southern ice caps were forming, and sea level was dropping. This was too much for the clunky, jawless fish, who were having trouble competing with their newly evolved and better equipped cousins. Most of them went extinct. But they weren't alone. The changing climate helped cause another mass extinction. The extinct groups stopped leaving fossils, and new groups began to leave more, leaving a record in the rocks of the transition from the Devonian to the Carboniferous.

THE CARBONIFEROUS: GIANT AMPHIBIANS, SEEDLESS SWAMPS

THE EARLY CARBONIFEROUS

The Carboniferous period has two subdivisions--the Early and Late Carboniferous, or in the United States, the Mississippian and the Pennsylvanian. The Carboniferous Period is named for the vast deposits of coal formed by ancient swamps. Most of this formed in the Late Carboniferous, and the Early Carboniferous produced more limestone than coal. The cooling at the end of the Devonian didn't last long, and the Early Carboniferous climate soon grew very warm. Rising seas covered the lowlands, where the calcium shells of aquatic animals accumulated to produce great shelves of limestone. Among the main producers of this limestone were crinoids, which began to diversify around this time. Limestones from this period are commonly full of washer-shaped rings that once joined to form the crinoids' stalked, branching body.

Amphibians found life on land to be full of opportunity, and they diversified accordingly. Like the early vascular plants, however, they were tied to the water, and for similar reasons–both needed a wet environment for reproduction. Early plants needed water for their sperm cells to swim through, and amphibians had to lay eggs in the water to keep them from drying out (as modern amphibians still do). From within the ranks of these two groups emerged two new groups that were able to solve these problem–seed-bearing plants and vertebrates that could lay waterproof eggs.

Seed plants had two adaptations that would prove very useful–seeds and pollen grains. While a spore is a single cell that grows into a multicellular, haploid plant, a seed contains a fertilized, diploid embryo, along with a supply of nutrients, all encased in a tough coating. This makes the seed much better equipped to weather tough conditions before germinating. When it does germinate, it will grow into a diploid plant, which is the dominant generation in seed plants. The haploid generation has been reduced to just a few cells contained within the diploid plant. Those around the egg form nutrient-rich tissue to feed the embryo, and those around the sperm formed another big innovation–a tough capsule for the sperm known as a pollen grain. Whereas earlier plants had to let their sperm swim through a film of water to find the egg, the first pollen grains were simply carried by the wind. Those that reach egg cells grow a tube toward the egg, depositing the sperm to form a fertilized seed.

The tetrapods also invented a means of leaving the water–the waterproof egg, which kept water inside, but let gases like oxygen and carbon dioxide pass through as needed. Since such an egg could be hidden away on dry land, it was less likely to be eaten by predators than naked amphibian eggs. This allowed more resources to be devoted to each egg, in the form of a large yolk for the growing embryo to live on. The embryo is covered by a membrane called the *amnion*, so all descendants of the first producers of waterproof eggs are called **amniotes**. As Figure .5 shows, reptiles, birds, and mammals are all amniotes[2], and the first amniotes resembled what we would call reptiles, with dry, scaly skin which allowed them to remain out of the water. The relationship between these groups is more complex than is commonly suspected, as we will see, and it is technically dubious to call the first amniotes reptiles. For convenience, I'm going to anyway.

THE LATE CARBONIFEROUS

The seed plants and reptiles had aces up their sleeves, but their time had not yet come.

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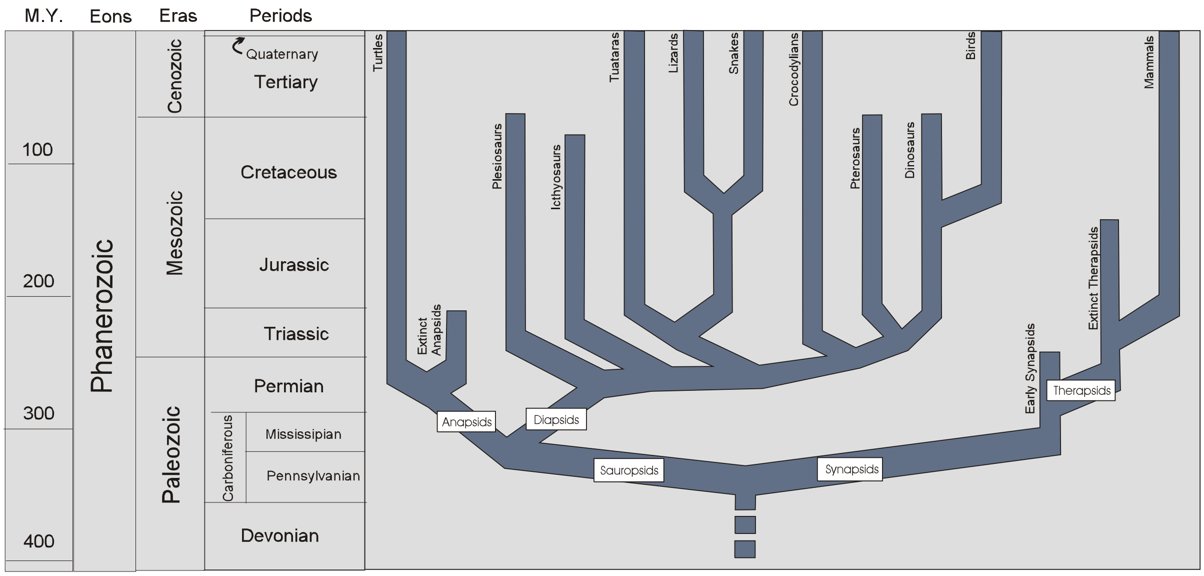
[2] Mammals usually incubate embryos inside their bodies, instead of in an egg. We are still amniotes, however, because we are descended from amniotes, and because our embryos are still covered by an amnion.

Figure .5 Amniotes (Reptiles, Birds, and Mammals)



The Late Carboniferous would be the heyday of amphibians and seedless plants. The continents of Gondwana and Laurasia were beginning to collide; the first step in forming the great super-continent of Pangea. The collision rejuvenated long-eroded mountains, raising them as high as the Himalayas. Today their worn remains can be seen in the Appalachians of North America, the highlands of Wales and Scotland, and in the fjord country of Norway. In the lowlands around the equator, dense, tropical swamp forests of clubmoss trees and fern trees flourished. When the densely-packed plants died, they fell into the acidic waters of the swamps, preserving them until they were eventually compacted into coal. This coal, and the iron ores that often appear nearby, would fuel the Industrial Revolution millions of years later. Diverse amphibians, giant millipedes, and early insects populated the swamps. The first creatures to fly were insects with fixed wings, such as the first dragonflies, some of which reached the size of crows. A new style of flying insect appeared a little late,r with wings that could be folded backward; out of the way. Flight further accelerated the insects spectacular rise to prominence. By the end of the Carboniferous, seed plants were also gaining a foothold, as the first conifers began to spread through the forests.

THE PERMIAN: AN EMPHATIC END OF AN ERA

As the Carboniferous period gave way to the Permian, ice sheets had begun to build up around the south pole, which was occupied by southern Pangea. Glacially-scraped rocks from this time remain in modern Africa and India. Forests were still mostly seedless, and falling sea levels had made them drier. Diverse communities of organisms flourished around great reefs, built mostly by sponges and bryozoans, not true corals. Toward the end of the Permian, the climate grew hotter and drier, forming red sandstones in vast, windswept deserts. A continent including present day Siberia and Kazakhstan collided with northeastern Pangea, creating the Ural mountains. Great flows of lava in present day Siberia attest to the extreme volcanic activity accompanying this union.

AMNIOTES: THE EGG CAME FIRST

The Permian Period saw the displacement of the amphibians by amniotes, so this is a good time to discuss the relationship between the various kinds of amniotes. It is commonly said that both birds and mammals evolved from reptiles. This is basically true, except that it is technically rather difficult to say exactly where to draw the line between reptiles and their descendants. Like fish, reptiles are a successful and diverse group that has had time to develop lineages very different from its more typical members. This means that fish and reptiles are partly defined by exclusion–fish are vertebrates that are not tetropods, and reptiles are amniotes that are not birds or mammals. Such definitions do not sit well with biologists, who like to include all the descendants of a common ancestor in a phylogenetic group; not just some of them.

If we wanted to be perfectly phylogenetically correct, then, we would not divide the amniotes into reptiles, birds, and mammals, but into **sauropsids** and **synapsids**, as shown in Figure .5. Synapsids are the group that gave rise to mammals, although many of the first were non-mammalian "reptiles". Sauropsids can be divided into two groups: **Anapsids** and **Diapsids**. The difference between all these groups has to do with the number of holes they have in their skulls. A synapsid has one hole on each side of its head. We still have this hole, between our cheekbone and braincase. Diapsids have two holes on each side of their heads, and anapsids have no holes. One might expect a lack of holes in the head to be an advantage, but the anapsids proved to be the least successful of the amniotes. Turtles have been their only major success story.

This division helps clarify the fuzziness associated with the definition of a reptile. Many biologists only call sauropsids reptiles. This is somewhat counterintuitive, since the early synapsids were scaly, four-legged egg layers, which is what most people would call a reptile. And even if we only call sauropsids reptiles, we are including birds as reptiles. And technically speaking, they are reptiles; just highly modified reptiles. And this is not just a technicality, because crocodiles and dinosaurs are actually more closely related to birds than they are to turtles. With all that said, the traditional definitions of birds, reptiles and mammals are useful, and are surely here to stay. Just keep in mind that these categories don't have sharp boundaries.

With that out of the way, we can look at the history of the amniotes. The first amniotes to undergo a real radiation were our own kin, the synapsids. Synapsids evolved in late Carboniferous times, and by the Permian they were displacing the amphibians. The first synapsids often looked superficially like large lizards. Besides the single holes in their skull, they were distinguished from other reptiles by their differentiated teeth. While most reptiles have teeth that are all alike, synapsids have different kinds of teeth for different purposes. The first synapsids' teeth were only different in size- some were longer than others, but they were all pointy. Later synapsids developed molars for grinding and incisors for nipping. This specialization of tooth structure would be one of the main themes in synapsid evolution, reaching its fullest expression in the mammals.

The first synapsids were a group called *pelycosaurs*. Many of these were large creatures; about the size of today's komodo dragons. Some sported fanlike sails on their backs, which seem to have functioned in temperature regulation. The pelycosaurs probably turned the broad side of their sails toward the sun in the morning to warm up, and into the wind and out of the sun later in the day to cool off. As the Permian went on, the pelycosaurs began to be replaced by another group of synapsids, the **therapsids**. Therapsid means "mammal arch", indicating that the skull had come to more closely resemble that of modern mammals (the only therapsids remaining today). Therapsids held their legs underneath their bodies, instead of out to the side as the first tetropods had, and as modern lizards, alligators, and salamanders still do. Most of the therapsids, and all of the pelycosaurs, were wiped out in the great extinction that ended the Permian period

This cataclysmic event killed off 96% of all species on Earth. Marine animals were hit especially hard. Every major marine group was diminished, especially the corals, and the trilobites disappeared entirely. Only molluscs emerged relatively unscathed. On land, most of the great forests disappeared, along with most (but luckily not all) of the newly diverse synapsids. As severe as the Permian extinction was, scientists are still not sure what caused it. Carbon dioxide and other gases from the Siberian volcanoes may have reached poisonous levels, and volcanic clouds may have blocked sunlight. The formation of Pangea reduced the amount of coastline, which may have contributed to the extinction through habitat loss. Sea levels and climate may have fluctuated wildly. Perhaps an asteroid collided with the Earth. There seems to be no consensus, but whatever the reason, the Paleozoic Era had come to an abrupt end.

MIDDLE AGES: THE MESOZOIC

THE TRIASSIC: REFILLING THE DESERTS

Geologically, the Triassic Period was very much like the Permian. All the continents were united as Pangea, while the other half of the Earth was covered by the great Panthalassa ocean. Pangea was so huge that moisture seldom found its way into the interior which was mostly red desert. The desert scene was intensified by the relative lack of life at the dawn of the Triassic. The great forests of the late Paleozoic had all but vanished, as had many of the animals and other consumers that depended on them. The seas were also desolate at first, populated mostly by molluscs.

This great biological vacuum would soon be filled, however. True coral animals soon made a comeback, taking over more of the reef building trade. As the Triassic progressed, the scattered clubmoss forests gave way to thin forests of seed ferns (now extinct). These, in turn, gave way to other seed plants, such as ginkgos, cycads, and especially conifers. All of these are **gymnosperms**, which means “naked seed”. They are so called because they leave their seeds exposed. A conifer, such as a pine tree, has seeds sitting between the scales of its cones. When the seed are fertilized, they will fall out, often blowing away on the wind on hang-glider wings. **Angiosperms**, the other great division of seed plants, keep their seeds tucked away until they are ready to distribute them. But these had not yet evolved, and the forests were ruled by the gymnosperms.

Among the few groups of therapsids to survive the Permian extinction were the **cynodonts**, or "dog tooths". As the name suggests, cynodonts had highly differentiated teeth rather like a dog's. In fact, cynodonts had a whole suite of modifications to their skulls, including large synapsid openings, flared cheekbones, and a so-called *secondary palate*, which separates the nasal cavity from the mouth. This allowed the cynodonts to breathe more efficiently, especially when eating. Efficient breathing was becoming more necessary because cynodonts were becoming warm blooded creatures; able to maintain a relatively constant body temperature. This is a useful adaptation for animals with active lifestyles, but it relies on a high metabolic rate, which requires lots of food and oxygen.

DOMINANT DIAPSIDS AND HUMBLE MAMMALS

Many of the early cynodonts were large, active carnivores, about the size of dogs. After the Permian extinction, most cynodonts grew smaller. Since smaller animals have a harder time maintaining a constant body temperature, these small cynodonts began to grow hair between their scales for insulation, and developed sweat glands for cooling off. By the late Triassic, some of these small cynodonts had a new kind of jaw. While most reptiles have jawbones made of more than one bone, these had jaws with just one. The other bones had shrunk, remaining as the tiny bones within the ear. In a rather bizarre adaptation, sweat glands along the abdomen became modified to produce a nutritious substance–milk. With these new **mammary glands**, as well as the modified jaws, the first mammals had arrived.

But they made no big splash at the time. They scurried into the shadows, as the rest of the cynodonts began declining toward extinction. The synapsids were giving way to the sauropsid reptiles, especially the diapsids. Some diapsids took to the seas. Among them were the icthyosaurs, which were shaped almost identically to today's dolphins. This similarity is one of nature's finest examples of the phenomenon of **convergent evolution**–where unrelated organisms filling similar niches acquire similar forms. Some reptiles took to the skies; first as small gliding creatures, then as the *pterosaurs*, which could truly fly. Some pterosaurs would attain 12 meter wingspans. The ancestors of crocodiles and alligators found a stable niche as carnivores dividing their time between the land and water. They have occupied that niche ever since. Of course, the diapsid reptiles which would prove to be the most spectacular, if not the most durable, were the dinosaurs, which appeared midway through the Triassic. But they had not yet diversified, so we will return to them later.

JURASSIC: DINOSAURS AND FRACTURED CONTINENTS

Pangea did not last long. By the beginning of the Jurassic it had begun to fracture. The core of Eurasia began to pull away from northern Pangea, with the newborn Atlantic Ocean widening between the two. Great fractures, called **rifts**, outlined today's continents for the first time. Rifts often form great valleys that split off in three directions from a central point. Often these valleys fill with water, creating lakes or narrow seas. Africa is currently splitting apart in just such a rift. Two of the valleys have filled with water to form the Red Sea and the Gulf of Aden, which separate the African mainland from the Arabian Peninsula. The third valley extends into the African mainland as the Great Rift Valley, parts of which are filled to form large lakes such as Lake Tanganyika. During the Jurassic, such a three-way rift was just beginning, which would one day separate Africa, North America, and South America. While this was mostly a period of rifting instead of joining, the western edges of North and South America grew larger as islands and volcanoes were pushed up against them by oceanic plates, raising the ancestral Rockies and Andes.

In the forests, seed ferns died out, and cycads expanded. The cycads are still with us. They look superficially like palms, although they don't bear flowers, as true palm trees do. A new assemblage of reptiles expanded after the Triassic extinction, dominated by the dinosaurs. (Discuss)

A different type of huge reptile, the Plesiosaurs, hunted in the seas. These look familiar to most people, because they look just like representations of the Loch Ness Monster, a mythical beast whose image has evolved into that of an ancient reptile. The Jurassic Period also produced one of the most spectacular fossils ever found. This creature, called Archaeopteryx, looks like a cross between a bird and a dinosaur. And that is exactly what it is, since birds evolved from dinosaurs in the Jurassic Period. They would prove to be quite successful later on, and today they are the only living descendants of the dinosaurs.

THE CRETACEOUS: CLIMAX OF THE MESOZOIC

The world began to look much more familiar during the Cretaceous. All the continents were recognizable, except perhaps Australia and Antarctica, which were just beginning to separate. Antarctica was green instead of white, because it was not covering the south pole, and because the Cretaceous climate was warm and even. Arabia was joined to Africa, while India was all alone in the middle of the ocean. Shallow seas covered the lowlands of North America and Europe, and divided Africa right across what is now the Sahara desert. These seas gave the Cretaceous Period gets its name, which is Latin for “chalky”. Chalk is a very fine-grained limestone, and most of the world’s chalk was laid down in shallow Cretaceous seas. The most famous chalk deposit forms the white cliffs of Dover, in England. Much of the world’s oil, especially that around the Persian Gulf, comes from the Cretaceous Period, where it formed from organic matter in deep waters.

Biologically, it was a very different world from our own. The dinosaurs and various other prodigious reptiles were having their heyday. New kinds of organisms were also arising. New types of bony fish diversified, as did calcium-bearing plankton. The first mammals to bear live young evolved. First came the marsupials, which bear helpless babies and then tuck them away in a pouch. Then came the placental mammals, which let their babies develop longer inside the womb. These were useful innovations, but the reptiles had the ecological markets cornered, so the mammals were still rather insignificant.

The greatest success story of the Cretaceous would prove to be the flowering plants, or **angiosperms**, which began to diversify as soon as they evolved. One secret of their success is revealed in the name “Angiosperm”, which is Greek for “seed container”. Flowers enclose their seeds (or eggs, before fertilization) in a container called an **ovary** (Figure 6 **Awaiting permission for image**). The ovary is connected by a stalk, called a **style**, to a sticky head called a **stigma**. This whole structure is called a **carpel**. The stigma’s stickiness helps it capture pollen grains, which are produced by organs called **stamens**. When a pollen grain reaches the stigma, it grows a tube down through the style to fertilize the eggs, producing a seed, which begins to develop inside the ovary.

Now, plants often fertilize themselves, but it is best if different plants fertilize each other, at least occasionally. This is why many flowers are arranged so that pollen from the stamens can't easily reach the stigma of the same flower. In fact, many flowers are either male or female, with only stamens or styles. Sometimes a single plant has both, and sometimes an entire plant may be either male or female. Now, for separate plants to pollinate each other, the problem is to get pollen from the stamens of one plant to the stigmas of another. This is where the colorful **petals** come in. Whereas gymnosperms rely on the wind to carry pollen, most flowering plants recruit animals, mainly insects, to carry it straight from one plant to another. They accomplish this by enticing them with sweet, nutritious nectar, advertised with colorful petals (or sometimes **sepals**, which often look like green leaves just below the petals.) When the insect visits the flower in search of nectar, it picks up some of the sticky pollen grains. When it visits the next flower, some of these grains may come off on the stigma, fertilizing the seeds.

Oftentimes, flowering plants recruit animals to spread these seeds. When the ovary is fertilized, it changes shape to become a **fruit**. Some fruits, like grapes, apples, and berries, are quite tasty when they are ripe and they advertise their ripeness with a splash of color. This attracts animals, who carry the fruit away. Oftentimes, they carry it away internally, after they have eaten it. The indigestible seeds pass straight though the animal's digestive tract, emerging along with a bit of fertilizer. Some fruits disperse themselves in different ways. Many dry up and become hard. Some grow hooks, to catch a ride on passing animals. Some grow wings or tassels, catching the wind and gliding away.

As soon as flowers evolved, they began to co-evolve with insects. They developed attractive colors, and arranged their flowers just so for rubbing pollen on and off their visiting accomplices. Many flowers formed associations with particular kinds of insect. Some are mainly pollinated by bees, while other are adapted to moths or butterflies. Other plants became adapted to pollination by birds. Insects cannot see red well, so many red flowers are pollinated by hummingbirds. Some large white flowers, such as moonflowers, open at night to be pollinated by bats and moths. By the end of the Cretaceous, flowering plants had exploded in diversity, replacing many of the gymnosperms and older styles of plant. The insects diversified along with them, though they had been expanding for some time anyway.

Most of the Cretaceous was a fine time for life on Earth. The climate was good, and the separating continents and extensive continental shelves offered myriad niches for living things to expand into. Each isolated continent began to evolve its own distinctive flora and fauna, which added to the diversity. But the Cretaceous ended badly, with another mass extinction that killed off the dinosaurs and many other groups. The chief suspect in this extinction is a meteorite, around 10 kilometers across, that struck the Gulf of Mexico just above the Yucatan Peninsula at this time. The debris from the impact blasted across North America, then filled the atmosphere around the globe, cutting of sunlight and causing acid rain. Shock waves may have set off volcanic eruptions as far away as India. This tremendous wallop must have been cataclysmic for most organisms living at the time, but some scientists think other factors may have contributed to the extinction. Many groups of organisms, including the dinosaurs, may have been declining for a few million years before the impact. Others, such as the mammals, had begun to diversify. It may be that the meteorite administered the coup de gras to species that were already failing. In any case, the Cretaceous extinction drew the curtain on the Mesozoic Era. The Cenozoic Era would have a fresh cast of characters.

RECENT TIMES: THE CENOZOIC ERA

THE TERTIARY PERIOD: A NEW CAST OF CHARACTERS

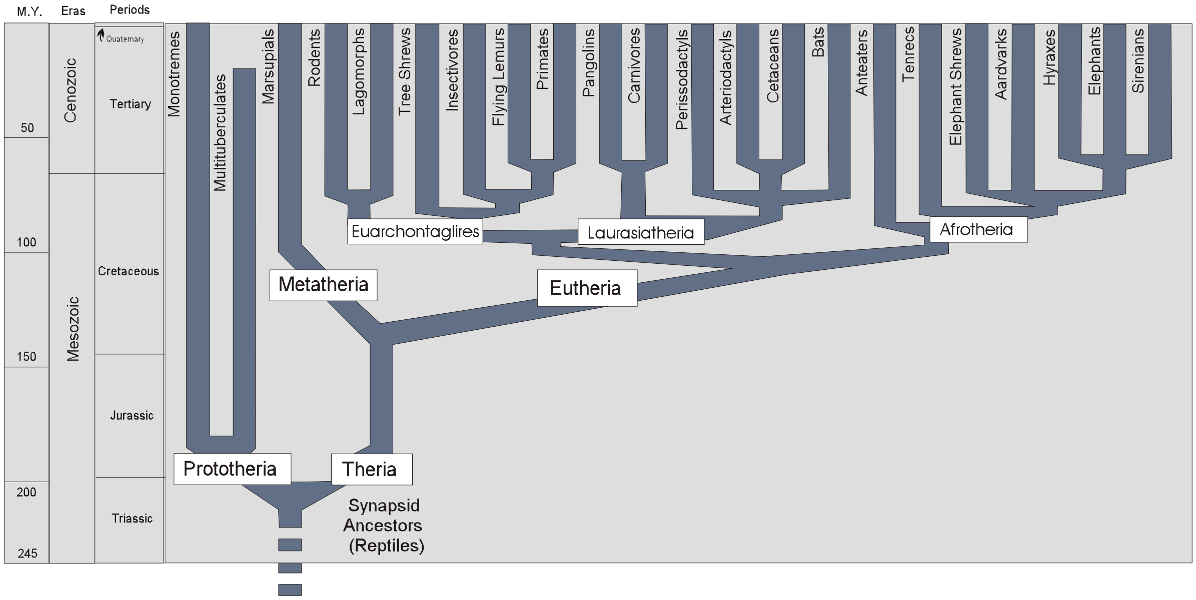
The Cenozoic Era is divided into two periods. The Tertiary Period lasted for 63 million years, while the Quaternary–the period in which we live–has thus far lasted only 1.8 million years. The world was very warm at the beginning of the Tertiary Period, with widespread tropical forests; full of the new flowering plants and quickly filling with mammals, birds, and as always, more insects. New reef communities were forming along the coasts, with the modern style of coral animals as the new reef builders. Many of the continents were acquiring the features we know today. The Rocky Mountains were rising in western North America, and the Andes in South America. The Alps and Pyrenees lifted and welded Europe, as blocks of land containing present day Spain, Italy, and Greece joined the mainland. While the Atlantic Ocean continued to widen, the “ring of fire” around the Pacific ocean formed, as new subduction zones emerged. India began to drift toward Asia. The collision would raise the high Himalayas, Earth’s youngest and most rugged mountain range.

The Cenozoic Era is often called the “Age of Mammals”. This is an accurate, but limited, assessment. Mammals did explode into niches vacated by extinct groups, but so did birds, modern amphibians, and bony fish. Flowering plants continued an explosion that had begun at the end of the Mesozoic, and this, in turn, shifted the expansion of insects from rapid to explosive. Mammals are not the only story of the Cretaceous. Nevertheless, since we are mammals, and mammals have been one of the premiere groups of the Cenozoic, so let’s take a closer look at their family tree.

The history of mammals in the Cenozoic Era is literally the textbook example of an adaptive radiation. After coasting through most of the Mesozoic Era, mammal diversity suddenly exploded, as Figure .7 shows. Interestingly, this radiation clearly began before the Cretaceous Period ended, which means that the mammals didn’t just expand into niches vacated by the extinguished reptiles. It may be that mammals had begun to compete with reptiles toward the end of the Cretaceous, helping cause the apparent decline leading up to the great extinction. Some have suggested that mammals began feeding on reptile eggs. Such behavior can deal a terrible blow to the egg-laying population, as humans have frequently demonstrated by harvesting wild bird eggs. Whatever their secret, mammals represented a spectacular comeback for the synapsid branch of the amniote tree.

But mammals had been in the minor leagues for a long time before getting bumped up to the majors, and we need to look back into the Mesozoic to see how the major divisions arose. Shortly after mammals evolved, in the early Mesozoic, they split into two groups: the **Prototherians** and the **Therians**. Prototherians still laid eggs, as their ancestors had done. While they had milk glands, they had no nipples. The milk simply oozed out for the babies to lap up. There were several lines of prototherians, including a widespread, rodent-like group called the

Figure .7 Possible Evolutionary History of Mammals



multituberculates, but the only remaining prototherians are two species of *monotremes*–the echidna, which resembles a hedgehog, and the duckbill platypus, which resembles the love child of a beaver and a duck.

The other group of mammals, the therians, do not lay eggs. They incubate their young inside their body. How long they do so is the basis of the next division in the mammal lineage. Therians are divided into **Metatherians** and **Eutherians**. Metatherians, or marsupials, give birth to tiny, undeveloped young, who crawl into a pouch on the mother's belly, attach themselves to a nipple, and keep developing. Eutherians let their babies cook a little longer, so they are born much more developed at birth. Except around Australia, the vast majority of mammals today are eutherians. Australian mammals show the impact that isolation of continents can have on evolving populations. It has been isolated for so long that marsupials there have radiated to fill niches that were filled by eutherian mammals on other continents. This has produced some striking examples of convergent evolution, as creatures from different lineages acquired similar forms. The recently extinct *thylacine*, or marsupial wolf, looked just like members of the eutherian dog family, and one would never guess that the marsupial mole is quite unrelated to other moles of the world.

The separate, but parallel, evolution of mammal groups in Australia and the rest of the world has long been obvious. More recently, scientists have discovered that mammals have evolved separately on other continents. As figure shows, eutherian mammals are divided into four major groups: **Euarchontaglires**, **Laurasiatheria**, **Xenarthra**, and **Afrotheria**. The Euarchontoglires includes the primates, rodents, and associated groups. Laurasiatheria is a diverse group including carnivores, bats, hooved animals, whales, and various insect eating mammals. Both of these groups originated in the Northern Hemisphere, either in North America or Eurasia. The xenarthrans (anteaters, sloths, and armadillos) and the afrotherians (which include elephants, manatees, aardvaarks, and various small insect-eaters) both originated in Africa. It seems, then, that mammals evolved on separate courses in Africa and the northern continents (South America, like Australia, was originally populated mostly by marsupials). Here again, convergent evolution has produced astounding similarities. For example, moles have evolved separately in both lineages. This means that burrowing insect eaters have evolved three separate times, suggesting that there is a very deep "mole attractor" in mammal evolution. As the Cenozoic progressed, the various groups of mammals found their way to different continents. Primates, for example, have mostly moved to the Southern Hemisphere. Hooved mammals, carnivores, and rodents spread to most continents, and the highly mobile bats spread and diversified all over the world.

Notice that I haven't discussed the evolution of mammals in Antarctica. That's because there aren't any there, except for aquatic ones offshore. It's too cold. This frigidity, like mammal evolution, is also a product of the arrangement of the continents. Antarctica and Australia began to move apart about 40 million years ago. Australia moved toward warmer regions, while Antarctica began to take its current place over the south pole. The split between the two continents allowed cold ocean currents to circulate unhindered around Antarctica. Ice caps began to spread across the continent, and deep currents of cold water began to flow from the south. The Earth had begun to enter one of its periodic cold snaps.

As it grew cooler, the climate also became drier. This favored a new type of flowering plant–grass. Most people don't associate grass with flowers, because its flowers are small and drab. It is pollinated by the wind, which doesn't care about nectar or bright colors. Grass has two very useful traits. First, it does well in fairly arid conditions. Second, it grows from its base, not from its tips. This means that it is not hurt by grazing animals, or more recently, lawnmowers. The first grasslands began to spread about 28 million years ago, pushing back many of the forests. This new ecosystem brought the continental flora much closer to its modern character–with forests in the wetter places, grasslands where it was a bit drier, and deserts where it was driest of all. The grasslands supported huge herds of migrating herbivores, such as elephants, single-hoofed mammals such as horses and rhinoceroses, and cloven hoofed mammals such as buffalo and antelope. Carnivores like wolves and lions followed these great herds, picking off the weak and less vigilant.

As the cooling trend continued, the Antarctic ice sheet grew larger, and worldwide sea levels dropped. The Mediterranean was briefly cut off from the Atlantic Ocean and evaporated, leaving a deep, salt-coated basin behind–something like an enormous version of Death Valley. Then, about 3 million years ago, the plate that underlies the Caribbean formed a land bridge between North and South America, at the Isthmus of Panama. This reunited animals and plants that had been evolving on separate courses since the breakup of Pangea. Porcupines, opossums, and giant ground sloths the size of hippopotamuses migrated northward. Far more species, for some reason, moved southward–bears, saber-toothed cats, various rodents, and even creatures no longer indigenous to North America, such as prehistoric camels, elephants, and rhinoceroses. The union of North and South America had other consequences. Ocean currents carrying warm water northward were disrupted, resulting in a buildup of ice around the North Pole (an uncommon situation in Earth's history). The climate grew still colder, and glaciers began to extend far into northern Asia, Europe, and North America. An ice age had descended on the Earth, and the Quaternary Period had begun.

THE QUATERNARY: INTO THE ICE AGE

THE PLEISTOCENE EPOCH: GLACIAL RHYTHMS

The Quaternary Period is a relatively short span of time, short enough that we need to zoom in a great deal to focus on it, as Figure shows. The Quaternary can be divided into two parts, called **epochs**. The first, the Pleistocene Epoch, was by far the longest; lasting 1.8 million years. The most recent epoch, the one in which we currently live, is called the Holocene. The Holocene began about 10,000 years ago, and continues to the present day. Ten thousand years may seem like a terribly short time to call an “epoch”, and perhaps it is, but it has been the scene of some rather momentous events. We will get to these, but let’s look at the Pleistocene first.

As Figure shows, the Pleistocene was seized by a severe ice age, with enormous continental glaciers at both ends of the Earth. The amount of glaciation fluctuates sharply, however. Most of the time, great ice sheets extend down into North America, northern Europe, and northern Asia, covering the sites of modern cities such as Chicago, London, and Moscow. They also cover high mountain ranges such as the Rockies, Alps, Urals, Himalayas, and southern Andes. These **glacial cycles** last for about 100,000 years, interrupted by warm periods called **interglacials**, during which the glaciers recede for 10 to 15 thousand years. You may have noticed I have switched to the present tense. This is because the ice age is still going on. We just happen to be living in one of the warm periods; a short glacial coffee break.

The ice sheets of the Pleistocene have shaped the modern landscape greatly. Glaciers have scoured the landscape every time they have descended, picking up rocks, dragging them along, and then dropping them. This gives glaciated landscapes a scraped look, often with scattered boulders that seem to have been dropped at random. Glaciers plow up great mounds of earth called *moraines*. Small moraines are visible in glaciated mountain valleys. The continental glaciers left rather larger moraines, such as the ones in the eastern United States now known as Cape Cod and Long Island. Alpine glaciers carved the high mountains, giving many of them sharp peaks and U-shaped valleys. In places like Norway, such valleys have filled to become fjords. The melting ice of receding glaciers created lakes. Some are small and numerous, like the many lakes of Minnosota, Ontario, and Finland; and some are huge, like the Great Lakes of North America. The pressure underneath the continental ice sheets was intense. Where it was thickest, it actually pressed the continental crust itself downward. Hudson Bay and the Baltic Sea both sit in depressions formed by the heaviest parts of the ice sheets. Parts of the British Isles are still rising after being unburdened by the current thaw.

The living world was transformed as much as the landscape during the Pleistocene. Tundra ecosystems formed around the edges of the ice sheets. Here, the vegetation is made up mainly of moss, lichens, and dwarf trees. Further south, the tundra gives way to northern coniferous forests of spruce, fir, and pine. These give way to broadleaf forests farther south, or grasslands in dryer areas. As the ice has advanced and receded throughout the Pleistocene, these ecosystems have marched northward and southward. During the last glacial cycle, for example, tundra extended as far south as the French Riviera. The Pleistocene also produced distinctive, well-insulated types of animals, such as wooly mammoths and wooly rhinoceroses, which are now extinct, as well as bison and musk ox, which are still around.

THE HOLOCENE

The peak of the last glacial cycle was about 18,000 years ago. After that, the glaciers began to recede, and retreated to roughly their current positions by about 10,000 years ago. The time since then is known as the Holocene. Geologically, the Holocene is just another interglacial period, and it would not be considered a separate epoch except that it is the one that modern human societies happen to have emerged in. That may seem like one of the biases I have been railing against. But it isn't, as we will see.

By a few thousand years after the end of the last glacial cycle, the natural world had emerged in its modern form. Figure .8 (**Awaiting permission for image**) shows the natural vegetation of the Holocene world, which probably closely resembles that of any Quaternary interglacial period. The northern ice is confined to pack ice on the Arctic Ocean, with the ice sheet of Greenland the only reminder of the great northern ice sheets. The tundra lining the northern edges of North America and Eurasia give way to vast evergreen forests. Great deciduous forests covered temperate areas near oceans, such as the southeastern United States, much of Europe, eastern China and Australia, and New Zealand. Mid-latitude areas in the continental interiors formed temperate grasslands, as in Australia, the Asian steppes, the great plains of North America, and the Argentine Pampas. The driest areas, of course, are deserts. Near the equator, wet areas form the vast tropical rain forests of Central and South America, Africa, and the stretch from India to New Guinea. Drier tropical areas form savannas, which stretch across most of Africa.

Of course, as we have seen throughout this chapter, many living communities are aquatic. The rivers and lakes of the continents support great freshwater ecosystems. Where the rivers meet the oceans, unique ecosystems thrive in estuaries. Offshore, there are benthic communities of the seafloor, mainly along the continental shelves. Great reefs form in warm waters, such as the Carribean, Northern Australia, and the equatorial Pacific. Finally, there are the great pelagic communities of the open water. These are richest above the continental shelves, but they spread across the entire oceans, making them the most widely distributed ecosystems on Earth.

This is a portrait of the natural world, at least as it looks in the interglacial periods. Since the Holocene is just one of several interglacial periods, it may seem a stretch to separate it as its own epoch. But it isn't, and here's why. The Holocene has not been just another interglacial period. The world today looks very different than figure , because of human impact. Many of the grasslands have been converted into croplands. The great deciduous forests have long since been fragmented, replaced by croplands, second-growth forests, tree farms, and cities and suburbs. The tropical forests are going the same way. The ocean realms have been greatly altered, with many of the sensitive coral reefs dying off from pollution and introduced species. Many of the enormous schools of fish, such as the cod of the North Atlantic, have all but vanished. The only biome that has flourished under our watch are the deserts, which have steadily encroached into areas that were once grasslands.

The Holocene is unique in all of Earth's history, because it is the only time that one species has changed things so much in such a vanishingly short time. That species is Homo sapiens, the species to which you and I belong. Biologically modern humans have only existed for 100,000 years or so; just 5 % of the Quaternary Period, which makes up about .04 % of the Earth's 4.55 billion year history. Our biggest impacts, however, have happened during the Holocene. To put this in perspective, if the Earth were a 30 year-old woman, the Holocene would have taken up the last 1.5 hours of her life. To see how we got in a position to have such a large impact in such a short time, we need to look at the emergence of brains and minds.