Chapter 11

History of Life

11.1 Lesson 11.1: Studying the History of Life

Lesson Objectives

- Use the conditions required for fossilization to explain why fossils are rare.
- List and give examples of different types of fossils.
- Discuss the way in which index fossils contribute to our understanding of the history of life.
- Compare relative dating of fossils and rock layers to absolute dating.
- Explain why "carbon dating" is an inadequate description of aging rocks and fossils.
- Describe how molecular clocks clarify evolutionary relationships.
- Compare and contrast Geologic Time with absolute time. Include limits of each.
- Sequence the levels of organization of the Geologic Time Scale from largest to smallest.
- Arrange the four major Eons and one Supereon from youngest to oldest.
- Describe and interpret the differences in fossil abundance throughout the Geologic Time Scale.
- Distinguish macroevolution from microevolution and explain their relationship.
- Describe the general pattern of the fossil record to support Darwin's idea that all life descended from a common ancestor.
- Evaluate the role of mass extinctions and episodic speciation in evolution.
- Identify types of major environmental change in the earth's history and relate them to patterns in the fossil record.
- Analyze ways in which the Geologic Time Scale may give false impressions of the history of life.
- Discuss rates of macroevolution and speciation, comparing and contrasting the ideas of gradualism, punctuated equilibrium and quantum evolution.
- Compare and contrast adaptive radiation (divergent evolution) to convergent evolution.

- Indicate some changes in geography which influence evolution.
- Use patterns of evolution and environmental change to account for worldwide differences in the distribution of mammals (placentals vs. marsupials).
- Define and give examples of coevolution.

Introduction

***"There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved."* - Charles Darwin, *Origin of Species.* 1859**

The history of life as we currently understand it is vast and wondrous and dramatic and humbling and ennobling. Vast is the almost unimaginable expanse of time during which life has flourished: four billion years is our current best estimate! Wondrous is the diversity of species throughout that time: some 30 million species occupy Earth today, and over 90% of all which have ever lived are extinct. Dramatic are the tales of change in environment and in diversity: ice ages, volcanism, continental drift, mass extinction, and bursts of evolutionary creativity have all shaped the natural environment. Humbling is the recognition that humans have played a relatively small part in the history; if the 4.6 billion-year story of Earth is reduced to a single **cosmological day,** humans occupy just the last minute and a half, and civilization covers less than the final second (**Figure** 11.1). Ennobling is the story's revelation that we are related to and interdependent with all other species – back 4 billion years to "so simple a beginning" (**Figure** 11.25). Finally, the history of life suggests we might add one more striking impression: Terrifying is the realization that we are in many ways unique among species in our unprecedented power to change the environment, influence evolution, and destroy life's diversity.

If we as a species occupy just the last minute and one-half of the cosmological day, how can we know the vast history of that 4.6 billion-year "day?" How did we arrive at 4.6 billion years as the age of the earth? How we know is the topic of this first lesson on the history of life.

Tools: The Fossil Record, Aging the Ages, and Molecular Clocks

By age three, you probably knew that dinosaurs are part of the history of life. Our understanding of where they belong in the tale is relatively recent, but "dragon bones" have been known for thousands of years in China and Europe. **Fossils** are preserved remains or traces of organisms that provide extremely rare but vivid windows to the past. Because most parts of organisms decompose rapidly following death, fossilization is an exceptionally uncommon

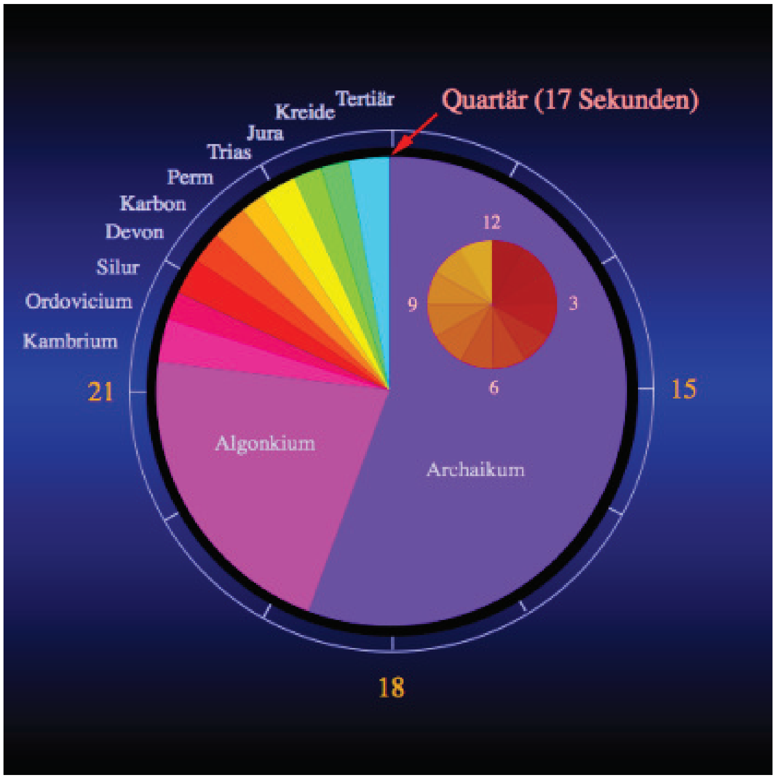

Figure 11.1: This Earth clock condenses the 4.5 billion years of earth's history into a single 24-hour day. German names mark major geologic time periods. The last 17 seconds comprise the Quaternary period, spanning the past 2 million years. Human civilization appears only in the last second of the clock's 24 hours. (19)

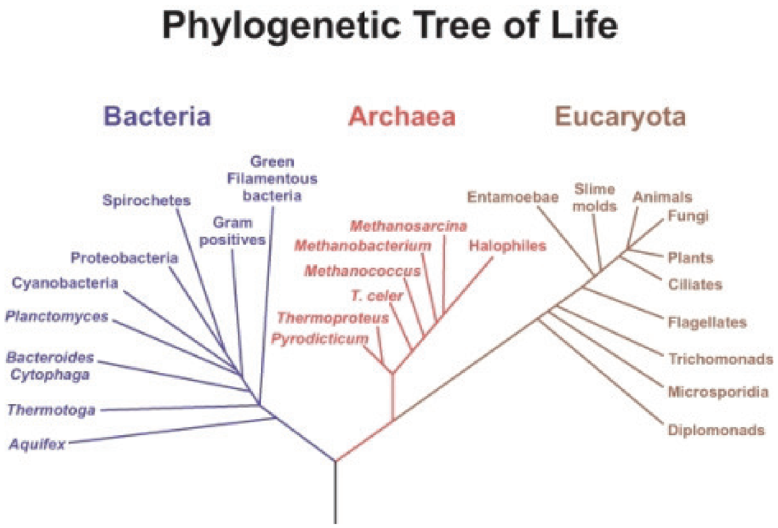

Figure 11.2: A family tree of living things summarizes our understanding of the history of life and shows that humans and animals share common ancestors with all of modern life. This diagram demonstrates our current understanding of evolutionary relationships. We will explore some of these relationships later in the chapter. (44)

occurrence, and usually preserves only hard body parts, shown in **Figure** 11.3. Remains must be covered by sediment almost immediately. Buried organisms may experience mineralization (occasionally even within cells), or they may decay, leaving a space within the sediment later replaced with rock. Alternative pathways to fossilization include freezing, drying, trapping in resin (amber) or burial in anoxic (oxygen-free) environments. **Trace fossils** preserve footprints, burrows, droppings, eggs, nests, and other types of impressions. Overall, a great variety of types of fossils reveal the history of life, shown in **Figure** 11.4.

Images in rock tell us what kinds of organisms lived in the past, but the story of life cannot be told without knowing when various organisms appeared. **Paleontologists** use two methods to date fossils. The oldest method looks at position within a sedimentary column of rock to give a fossil's **relative age**. If the rock layers are undisturbed, the deepest layers are the oldest, and layers near the surface are the youngest, shown in **Figure** 11.5. Widespread, short-lived **index fossils** can help identify rock layers of the same age spread around the earth, shown in **Figure** 11.6. Combining worldwide observations of relative position and composition resulted in a **Geologic Time Scale** for the Earth – a column of rock layers which reflects the history of sedimentary rock formation and changing life, stretching back to a time which apparently held no life. The fossil record showed patterns which, combined with his observations of living species, led Charles Darwin to conclude that all life on Earth descended from a single, simple common ancestor.

Relative age, however, only begins the story. **Absolute aging**, also known as **absolute dating**, uses **radioactive isotopes,** whose known **half-lives** can be used to calculate the

Figure 11.3: *Scipionyx samniticus* was a small dinosaur from Early Cretaceous Italy. This fossil of a juvenile only a few inches long is considered one of the most important vertebrate fossils ever discovered, because unlike most, it preserved internal organs as well as hard structures. Fossilization of an organism is itself a very rare event; preservation of soft tissues is even less likely. (16)

number of years which have elapsed since a rock formed. Radioactive decay is a random but exponential process. An isotope's half life gives the time period over which half of the material will decay to a different, relatively stable product, shown in **Figure** 11.7. The ratio of the original isotope to its decay product changes in a predictable way. This predictability allows the relative abundances of isotope and decay product to be used as a clock that measures the time from the incorporation of the isotope into a rock or a fossil to the present.

For example, half of a sample of Carbon-14 will decay to Nitrogen in 5,370 years. Cosmic rays cause the formation of Carbon-14 from the more common and stable Carbon-12 at a relatively constant rate, so carbon dioxide in the atmosphere contains relatively constant, predictable amounts. Organisms acquire carbon from various mechanisms – plants from CO_2, and animals and other heterotrophs through food chains. When an organism dies, its carbon intake stops, and existing Carbon-14 atoms decay exponentially, according to their 5,370-year half-life. The proportion of Carbon-14 in the organism's remains indicates the time lapsed since its death.

Table 11.1: **Isotopes Used to Measure Absolute Age of Rocks and Fossils**

Isotope	Decay Product	Half-life	Aging of Rocks or Fossils
Carbon-14	Nitrogen	5370 years	Up to 60,000 years
Uranium 238/235	Thorium/Protactinium	80,000/34,300 years	Hundreds of thousands of years

Table 11.1: (continued)

Isotope	Decay Product	Half-life	Aging of Rocks or Fossils
Potassium-40	Argon	1.3 billion years	Earth's oldest rocks
Uranium-238/235	Lead	4.5 billion /704 million years	1 million to > 4.5 billion years

Carbon-14 has a relatively short half-life, so its use for absolute dating is limited to a maximum of about 60,000 years. Other isotopes are used to reach deeper into geological time. Uranium-238 and Uranium-235 decay to different isotopes of lead with half-lives of 4.46 billion and 704 million years, respectively, and together allow dating of rocks between 1 million and over 4.5 billion years old. **Table** 11.1 shows some of the many isotopes can be used to study rocks throughout Earth's 4.6 billion year history.

Absolute aging techniques confirmed and brought into focus the rock layer story geologists and paleontologists had developed with relative dating. They pushed Earth's history back 4.6 billion years, and showed that complex life evolved after some two billion years in which bacteria alone populated the Earth.

Further confirmation of common ancestry included **molecular clocks,** which measure changes in DNA or proteins to indicate degrees of relationship among species. Comparing DNA sequences of several species of primates, for example, shows that chimpanzees are more closely related to humans than are gorillas or baboons, shown in **Table** 11.2. If we assume uniform rates of mutation, we can estimate not only degree of relationship, but time back to common ancestry. Because DNA sequences (and mutations) determine the sequence of amino acids in proteins, Hemoglobin and other proteins are also used as "clocks." Both DNA and protein clocks support a universal common ancestor for life, confirming the story which continues to unfold as new discoveries expand the fossil record. Molecular clocks, together with evidence from the fossil record, allows scientists to estimate how long ago various groups of organisms diverged evolutionarily from one another.

Table 11.2: **DNA "Clock" Comparison of Primates**

Species	% Difference in Nucleotide Sequence, Compared to Humans
Human	0
Chimpanzee	1.2
Gorilla	1.6
Baboon	6.6

Figure 11.4: Different types of fossils reveal the history of life. Clockwise from top left: Amber preserves an insect intact. Stone etches impressions of Edmontosaurus skin. Rock echoes a dinosaur's footprint. Fossilized eggs recall a dinosaur of Mongolia. LaBrea Tar Pits fossilized the remains of a rich diversity of ice age animals. Permafrost preserved this female mammoth calf for nearly 10,000 years. (17)

Figure 11.5: Relative aging dates sedimentary layers and the fossils they contain. Lower layers are older; upper layers are younger. Dinosaur fossils lie buried within this sedimentary formation in Green River, Utah. (51)

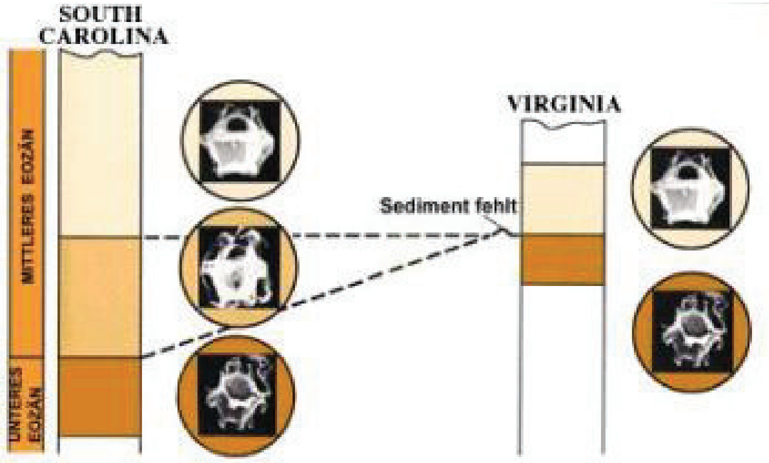

Figure 11.6: Single-celled algae serve as index fossils to correlate rock layers located in different states. The middle-aged rock layer in South Carolina has apparently eroded from a similar deposit of sedimentary rock in Virginia. Careful worldwide studies of relative age by many geologists and paleontologists led to the Geologic Time Scale. (26)

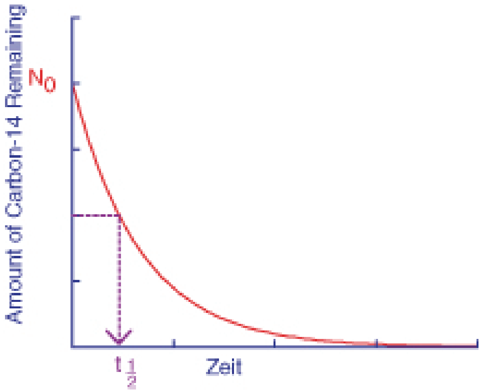

Figure 11.7: Exponential decay of a radioactive isotope such as carbon-14 occurs with a unique, predictable half-life (t½) of 5,370 years. The amount of carbon-14 remaining in a fossil organism thus indicates the time elapsed since death, giving a measure of absolute age. (13)

A Geologic Time Scale Measures the Evolution of Life

We noted in the previous section that observation of rock layers, dating techniques, and correlation of similar strata from around the world led to the development of a Geologic Time Scale (**Figure** 11.8). How does the scale divide 4.6 billion years of history? What themes emerge from its stories of the past?

One theme is almost unimaginable amounts of time. The deep time of Earth's history is far beyond our experience, and our knowledge is far more detailed for recent millennia than for the distant past. A scale divided into evenly spaced periods of time would not show that detail. Instead, Geologic Time Scale divisions mark major events which highlight changes in climate, geography, atmosphere, and life. The largest units of time are **Eons**. Eons include smaller **Eras**, which in turn include **Periods, Epochs**, and **Stages**. Faunal stages identify specific fossil groups. Terms such as Upper/Late and Lower/Early divide parts of the scale into more recent and more distant subunits.

Four eons comprise the history of Earth, and their names refer to a second major theme of Earth history: the evolution of life. The Phanerozoic ("visible life") Eon spans the most recent 545 million years and includes three Eras well known for their chronicle of life: the oldest Paleozoic, middle Mesozoic, and current Cenozoic. The Proterozoic ("before complex life") Eon precedes the Phanerozoic, extending back 2.5 billion years. The Archean ("ancient") and Hadean ("unseen") Eons reach back to the formation of the Earth. The Precambrian **Supereon** combines the oldest three eons, and refers to the time before the first great explosion of life recorded in the fossil record - the **Cambrian** Period. The name "Cambrian" refers to Wales, where these fossils were first studied. Before this first period of the Phanerozoic, animals lacked hard body parts to contribute to the fossil record.

Billions of years ago	Supereon	Eon	Era	Period	Epoch
Present		Phanerozoic	Cenozoic		Holocene/Pleistocene/Pliocene/Miocene/
					Oligocene/Eocene/Paleocene
			Mesozoic	Cretaceous/Jurassic/Triassic	
				Permian/ Carboniferous/	
0.5			Paleozoic	Devonian/Silurian/	
				Ordovician/Cambrian	
	PRECAMBRIAN	Proterozoic			
				Ediacaran	
1.0					
1.5					
2.0					
2.5		Archean			
3.0					
3.5					
		Hadean			
4.0					
4.5					
Origin	of Earth				

Figure 11.8: A linear arrangement of the Geologic Time Scale shows overall relationships between well-known time periods, which will be used in this and future chapters. Our knowledge of past life is concentrated in the most recent Eon, but the Phanerozoic occupies such a small proportion of the overall history of earth that eras, periods, and epochs are not precisely to scale. For future lessons, relevant parts of the scale will show more detail with greater accuracy. (20)

Patterns and Processes of Macroevolution

Throughout geologic time, the fossil record reveals dramatic changes in species and groups of species which have populated the Earth. Evolution at or above the species level is **macroevolution**, in contrast to **microevolution**, which describes changes within a species or population. Many scientists no longer emphasize the distinction, believing evolution to be a single process which includes both patterns. However, themes from the Geologic Time Scale illustrate macroevolution, so we will consider its patterns and processes in this chapter.

Although fossils dated back only to the Cambrian during Darwin's time, radiometric dating has since identified fossil bacteria as old as the beginning of the Archean era 3.5 billion years ago. The geologic record shows over 2 billion years during which the only life was unicellular. The appearance of eukarytoic cells roughly 1.8 billion years ago marked a dramatic increase in cellular complexity. In rocks 1 billion years old, multicellular eukaryotes begin to appear, and by the end of the Precambrian, fossils record a variety of ancient multicellular organisms. The beginning of Cambrian Period marks an "explosion" of life, and in general, biodiversity has increased throughout the Phanerozoic, shown in **Figure** 11.9. Our current understanding of the fossil record confirms Darwin's ideas that life began as tiny single-celled bacteria and over vast time evolved to produce the complexity and diversity we celebrate today.

As recorded in fossils, the evolution of life was not smooth or steady. **Mass extinctions** and **episodic speciation** interrupted the overall pattern of increasing biodiversity, shown in **Figure** 11.9. These disruptions reflect dramatic changes in the environment of the Earth.

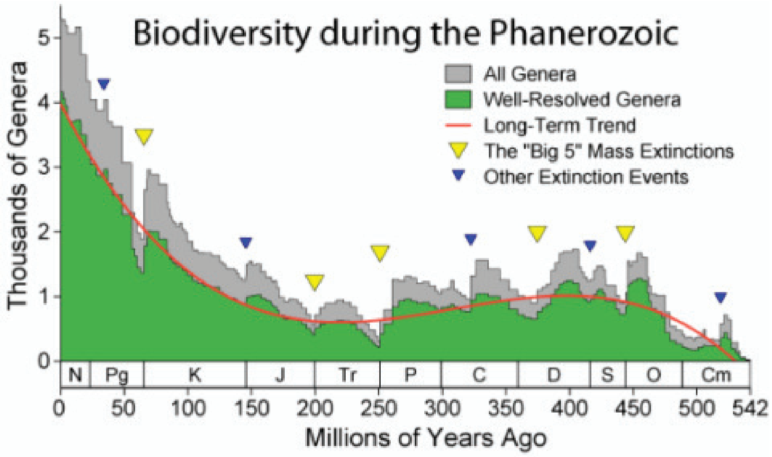

Figure 11.9: Estimates of numbers of marine genera throughout the last 542 million years support a gradual increase in biodiversity, interrupted by five major mass extinctions. Some scientists dispute the accuracy of such estimates, while others argue that they show regular cycles of extinction. (6)

A major theme of the fossil record is loss of species. The death of a species – **extinction** – seems to be as much a characteristic of life as the death of individual organisms. Both seem closely linked to change in environment. Through mutation or sexual reproduction, offspring show variation. Individuals whose variations are not well suited to their environment die. Those whose variations are adaptive survive to reproduce. Death and differential reproduction result in **adaptation** to a changing environment.

These same forces of **natural selection** inevitably affect species: the fossil record indicates that up to 99.9% of all species that have ever lived on Earth are now extinct. **Mass extinctions** involve most major groups of organisms over a short period. The past 550 million years, when fossils are sufficiently abundant to tell a reliable story, show five mass extinctions in which more than 50% of animal species died. The most famous is the extinction which ended the reign of the dinosaurs 65 million years ago. Accelerated evolution may follow mass extinction, because the empty ecological niches make way for new species. After the non-birdlike dinosaurs disappeared, mammals rapidly evolved to fill the available niches. The fossil record shows numerous examples of **episodic speciation**, a pattern of periodic increase which includes these rebounds as well as bursts of evolution following major new "discoveries" or "ideas" – for example, the biochemical pathways for photosynthesis or cellular respiration.

Closely related to mass extinction is the theme of major environmental change throughout Earth's history. Rock layers reflect critical changes in atmosphere and climate: oxidized iron deposits mark the introduction of oxygen gas to the atmosphere, and glacial deposits reflect periodic ice ages alternating with times of global warming. Craters and unique worldwide strata suggest that spectacular asteroid or comet collisions may have severely reduced solar radiation, and lava flows and ash suggests volcanism could have done the same. Massive geographic changes, now explained by **plate tectonics theory**, underlie volcanism as well as formation of new land bridges, seaways, and continents. Certain worldwide sedimentary deposits suggest significant sea level fluctuation, which may result from some of the aforementioned climate or plate tectonic changes. Life evolved against the backdrop of these often-catastrophic changes, and over 3.5 billion years of natural selection inevitably responded to them. Many of these changes are believed to have caused the mass extinctions and episodic speciation revealed in the fossil record. We will look at some of these events in more detail in the next two lessons.

Two caveats are critical in interpreting the history of life using the Geologic Time Scale. The first concerns the idea that evolution progresses via slow, steady, gradual change. We have already seen that mass extinction and episodic speciation interrupt the overall pattern of increasing biodiversity, but **gradualism** suggests that changes accumulate continuously as one species evolves to become another. An alternative, more recent theory, **punctuated equilibrium**, shown in **Figure** 11.10, proposes that species remain the same for long periods, and that change occurs infrequently but rather rapidly under unusual conditions such as geographic isolation or migration. The rather sudden appearance and disappearance of many individual species within the fossil record, noted even by Darwin, tends to support the latter theory. The idea of **quantum evolution** attempts to explain the origins of major groups (families, orders, and classes) as a response to drastic changes in environment or

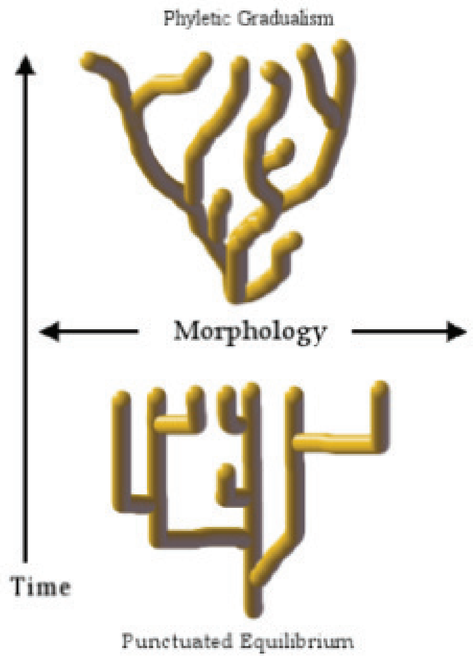

Figure 11.10: Two theories of evolutionary change - gradualism vs. punctuated equilibrium - are still debated. The former proposes continuous change, while the latter suggests that species remain constant for long periods of time and that change, when it occurs, is rapid. (49)

adaptive zones. The fossil record supports great variation in the rate of evolutionary change - from group to group and even among closely related lineages. Each of these ideas about pattern and rate may accurately describe one of many ways evolution works.

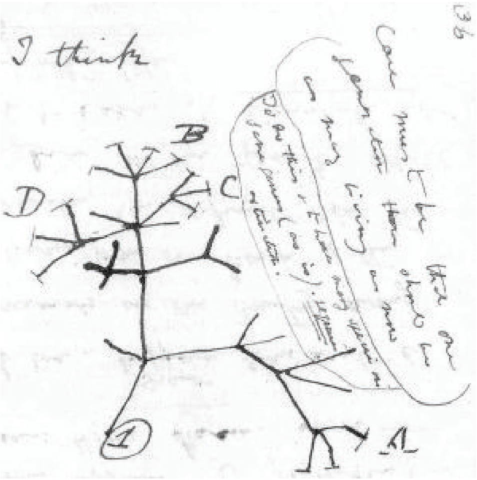

Figure 11.11: Charles Darwin's 1837 sketch from his First Notebook on Transmutation of Species (1837), shows the bush-like pattern of evolution. (30)

A second caveat: the 4.6 billion year time scale makes it tempting to view evolution as linear, and perhaps even goal-directed. Time may be an arrow, but evolution is much more a bush of common ancestry–a family tree, as we saw at the beginning of the chapter. Darwin recognized this - his sketch, shown in **Figure** 11.11, shows the pattern of speciation predicted by his theory of chance variation and adaptive selection. A very recent (August 2007) discovery encourages us to view our own human ancestry as a bush rather than a line. Radiometric dating of a new fossil of *Homo habilis* shows that this species coexisted with the "more advanced" Homo erectus, shown in **Figure** 11.12. Previously, scientists considered the former an ancestor of the latter. The inappropriate expression "more advanced" implies the false, linear, goal-directed interpretation of evolution.

A famous example of "bushiness" in the history of life is **adaptive radiation**, a type of **divergent evolution.** This pattern of speciation involves the relatively rapid evolution from a single species to several species which fill a diversity of available ecological niches. Mass extinctions (the dinosaurs!), new volcanic islands (the Galapagos, or Hawaii), land bridge formation (the isthmus between North and South America) or "invention" of a new idea in evolution – all are events which "suddenly" open a variety of niches for adaptive radiation. In each case, a fundamental structure in one species is modified to serve new functions in different environments or modes of life. For example, forelimbs of mammals have become elongated with grasping hands for the forested habitats of monkeys, flattened into flippers for the aquatic habitats of whales, and spread into wings for the aerial habitats of bats, shown in **Figure** 11.13. Adaptive radiation explains – and the fossil record shows – that these groups all arose from one ancestor or a small group of common ancestors.

Figure 11.12: Homo habilis (left) was considered an ancestor to Homo erectus (right) until the 2007 discovery of a habilis fossil which showed that the two species coexisted. The history of the genus Homo, like the evolution of most species, is undoubtedly more bush-like than linear. (5)

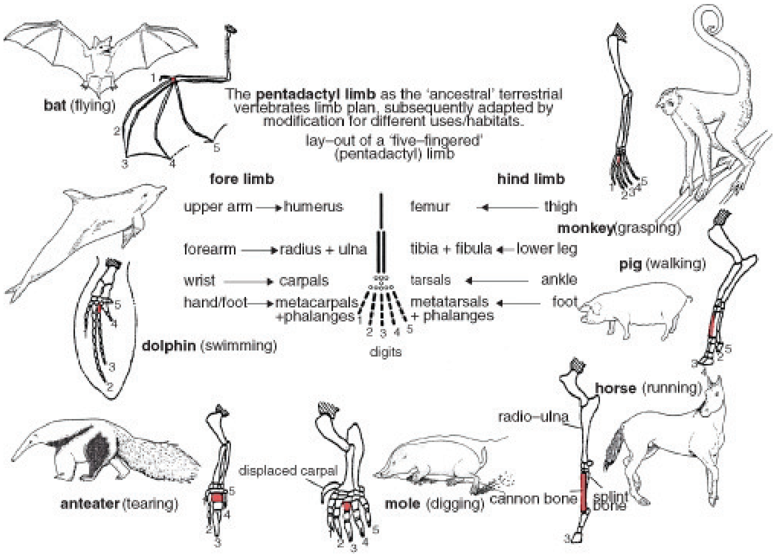

Figure 11.13: Forelimbs of mammals show adaptive radiation, or divergent evolution. Evolution has modified the original pattern in a common ancestor to suit a multitude of different environments. (1)

In contrast to divergent evolution, whereby closely related species evolve different traits, **convergent evolution** involves distantly related species evolving similar traits. This pattern surfaces frequently in the history of life when different organisms occupy similar ecological niches. For example, three major groups of organisms have evolved wings for flight: reptiles (pterosaurs), birds, and mammals (bats), shown in **Figure** 11.14.

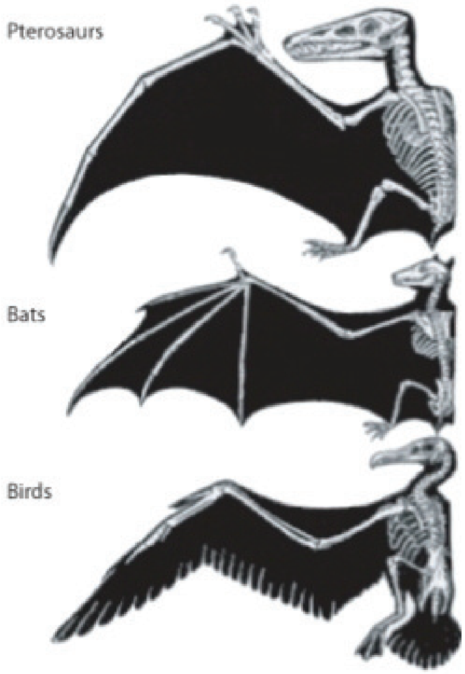

Figure 11.14: The wings of pterosaurs (1), bats (2) and birds (3) show convergent evolution. Similar structures adapt each group to flight, but each of the three types of wing evolved independently. (39)

Australian fauna reveal both divergent and convergent patterns related to major geographical change, shown in **Figure** 11.15. Major groups of mammals evolved in the northern hemisphere and migrated to Australia across a land bridge. Later submerging of the land bridge isolated the Australian mammals, and the marsupials underwent their own adaptive radiation within their insular continent. Elsewhere, placental mammals evolved to out-compete the more primitive monotremes and marsupials, and underwent their own adaptive radiation. These independent radiations resulted in some wonderful examples of convergent evolution: An example: the marsupial Tasmanian wolf (now extinct) shared with the placental canines many adaptations to life as a hunting predator, shown in **Figure** 11.16.

One last, fascinating pattern within the history of life is **coevolution**. In coevolution, two species or groups of species influence each other's evolution and therefore evolve in tandem. Relationships may be positive for one species or both, or an evolutionary arms race between predator and prey. Flowering plants depend on insects for pollination, so have evolved colors, shapes, scents, and even food supplies which are attractive to certain

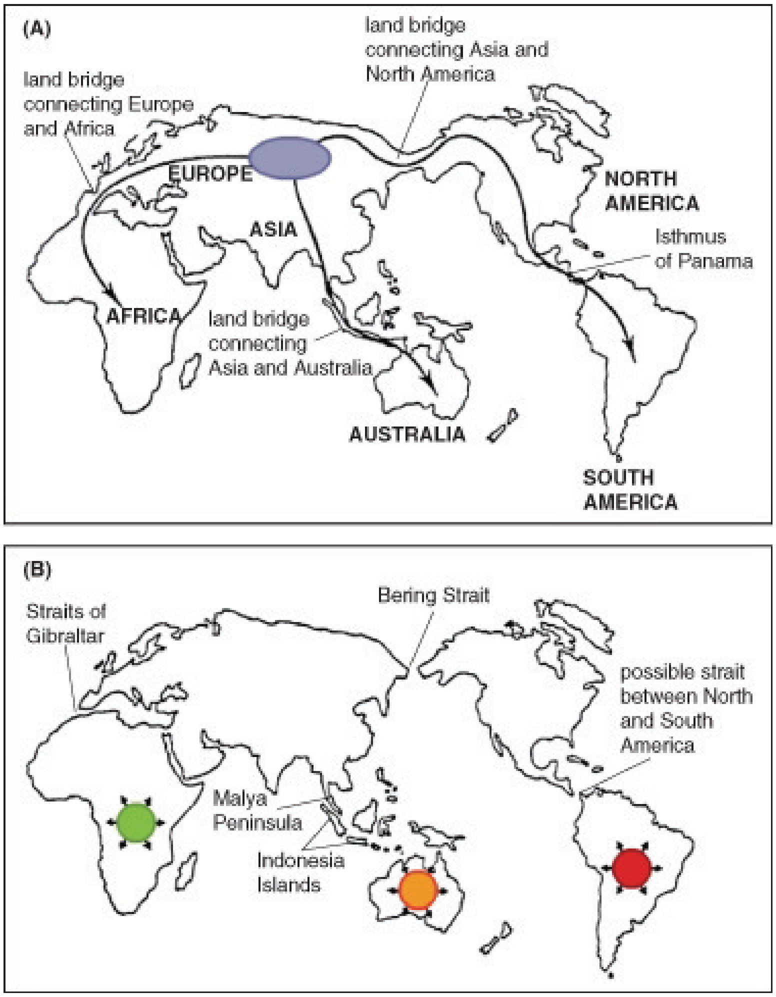

Figure 11.15: Australia's fauna demonstrates the importance of geography to evolution. Mammals evolved in the northern hemisphere and migrated to Australia across a land bridge (see A, above) which was later submerged (B). Marsupials persisted and underwent adaptive radiation in Australia. Elsewhere, the appearance of placental mammals spelled doom for the marsupials; placental mammals outcompeted them and underwent their own adaptive radiations. These separate radiations (green, orange, and red in B) resulted in a number of examples of convergent evolution. (18)

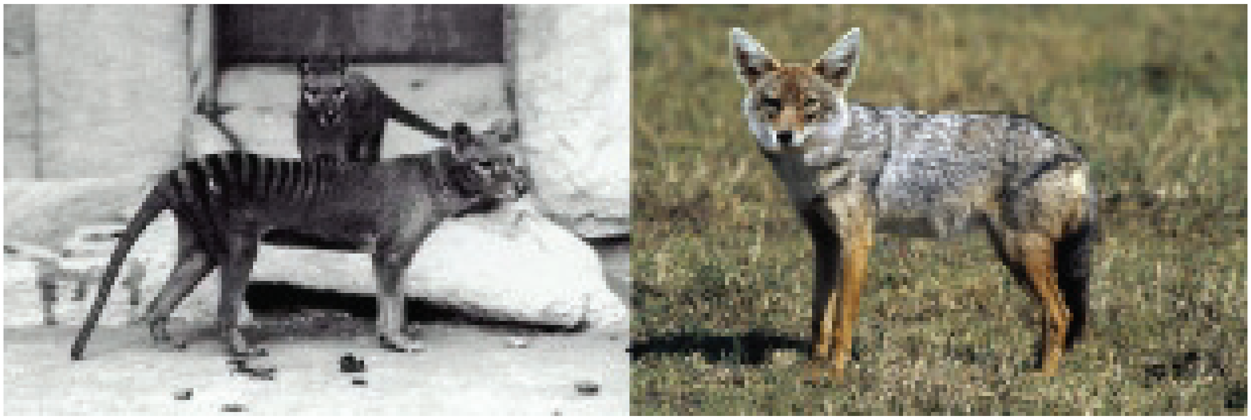

Figure 11.16: The thylacine or Tasmanian wolf, a marsupial, closely resembles the golden jackal, a placental canine; both show similar adaptations to predatory life, demonstrating convergent evolution. Marsupials and placentals evolved independently due to the loss of a land bridge connecting Australia to southeast Asia, so they provide examples of convergent evolution. (2)

insect species. Insects, in turn, have evolved mouthparts, senses, and flight patterns which allow them to respond to and benefit from specific floral "offerings," shown in **Figure** 11.17. The **Endosymbiotic Theory** describes a special form of co-evolution: Mitochondria and chloroplasts evolve within eukaryote cells, yet because these organelles have their own DNA sequence, different from that of the nucleus in the "host" cell, organelle and host cell evolve in tandem – each influences the evolution of the other.

Figure 11.17: Impressive proboscis and vivid colors! Hawk moths and the zinneas influence each other's evolution, because the flower depends on the moth for pollination, and the moth feeds on the flower. (46)

Closely related to coevolution is **coextinction**. If one member of a pair of interdependent species becomes extinct, the other is likely to follow. Famous examples were two species of bird lice which were obligate parasites on the passenger pigeon, shown in **Figure** 11.18.

When “Martha,” a resident at the Cincinnati Zoo thought to be the last passenger pigeon in the world died on September 1, 1914, the extinction of the bird lice species followed. Alas, one louse species was later rediscovered on a band-tailed pigeon, and the other species had been misidentified.

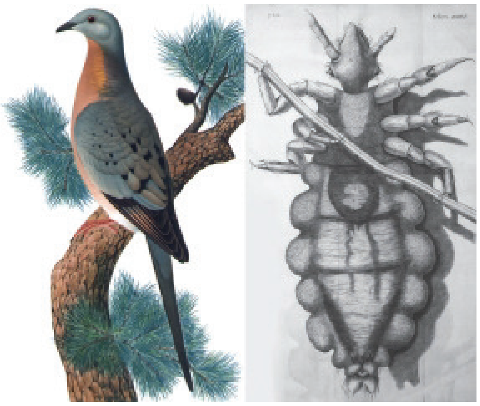

Figure 11.18: The passenger pigeon and a parasitic species of louse (not the one pictured above) demonstrate coevolution and potential coextinction. Each species influenced the other’s evolution, and when the host became extinct in 1914, the parasite narrowly escaped extinction only because an alternate host – the band-tailed pigeon – survived. (10)

In this lesson, you have explored the tools we use to study the history of life, the Geologic Time Scale which organizes what we know, and a variety of patterns found in the 4.6 billion year story. In the next lessons, look for examples of these patterns as we follow that story from the origin of life to what is becoming known as the Sixth Extinction today.

Lesson Summary

- If the history of life is condensed into a single 24-hour “cosmological day,” humans occupy only the last minute and one-half, and civilization, less than the final second.
- Fossils include mineralized remains of organisms, casts, impressions, footprints, burrows, droppings, eggs, or nests as well as frozen, dried, or amber-coated remains.
- The positions of fossils in rocks indicate their relative ages; older fossils and rock layers are deeper than fossils and rocks that are more recent.
- Radiometric dating measures the proportion of decay products of radioisotopes with known half-lives to estimate absolute age. Different isotopes with a range of half-lives cover the span of geologic time.
- Comparing DNA or protein in similar species can reveal evolutionary relationships and confirm patterns suggested by the fossil record.
- Geologic Time Scale divisions mark major events which highlight changes in climate, geography, atmosphere, and life.

- The largest units of time are Eons; the 4.6 billion years of earth's history are divided into four eons.
- The Phanerozoic includes the most recent 545 million years and the most detailed fossil record.
- Overall, the fossil record confirms Darwin's idea that life began as tiny single-celled bacteria and over time evolved to produce the complexity and diversity we celebrate today.
- Mass extinctions and episodic speciation interrupt an overall gradual increase in complexity and diversity.
- Evolution shows response to major environmental changes, including volcanism, continental drift, sustained warming and cooling, asteroid impact, and critical transformations of earth's atmosphere.
- The rate of evolution is not always uniform; gradualism does not characterize all speciation.
- The pattern of evolution is seldom linear, but rather more like a bush or family tree.
- Punctuated equilibrium, quantum evolution, and variable rates describe patterns of evolution which may differ from gradualism.
- In divergent evolution, also called adaptive radiation, closely related species evolve different traits to adapt to a variety of available niches.
- In convergent evolution, distantly related species evolve similar traits as adaptations to similar habitats.
- Geographic changes, including continental drift, affect patterns of evolution.

Review Questions

1. How do the conditions needed for fossilization explain the rarity of fossils?
2. Compare relative dating of fossils and rock layers to absolute dating.
3. Explain why "carbon dating" is an inadequate description of aging rocks and fossils.
4. Describe how molecular clocks clarify evolutionary relationships.
5. Compare and contrast Geologic Time with absolute time, including the limits of each.
6. Explain the ways in which the Geologic Time Scale and the fossils it records may be misleading concerning the history of life.
7. Construct a table or chart which shows five of the major patterns of macroevolution we have observed in the fossil record. Include the pattern name, a brief description or definition, causes or contributing factors (where applicable), and a specific example for each.
8. Explain how some of the patterns of evolution and environmental change account for worldwide differences in the distribution of mammals. Discuss placentals vs. marsupials.
9. Charles Darwin described an orchid from Madagascar that had a nectar well which measured 12 inches deep, keeping costly sugars far out of reach of all known butterflies and moths. He predicted the existence of a highly specialized pollinator moth with

a foot-long proboscis that could act as a straw to reach the nectar. After Darwin's death, scientists discovered a night-flying moth that matched Darwin's expectation and named it the "Predicta." Which pattern of evolution did Darwin see in the orchid? Explain why this is a good example of the pattern.

10. Relate human history to life's history, as shown in the Geologic Time Scale and fossil record.

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Vocabulary

absolute aging Measures half-lives of radioactive isotopes to calculate the number of years which have elapsed since a rock formed; also known as absolute dating.

adaptive radiation A pattern of speciation which involves the relatively rapid evolution from a single species to several species to fill a diversity of available ecological niches.

coevolution Evolution in which two species or groups of species influence each other's evolution and therefore evolve in tandem.

coextinction If one member of a pair of interdependent species becomes extinct, the other is likely to become extinct as well.

convergent evolution Evolution whereby distantly related species evolving similar traits.

divergent evolution Evolution whereby closely related species evolve different traits.

eons The largest units of time within the Geologic Time Scale; divided into eras, which are also divided into periods, epochs, and stages.

episodic speciation A pattern of periodic increase in new species; follows mass extinctions as well following major new "discoveries" or "ideas" – for example, the biochemical pathways for photosynthesis or cellular respiration.

extinction The death of an entire species.

fossils The preserved remains or traces of organisms; provide extremely rare but vivid windows to the past.

Geologic Time Scale A column of rock layers which reflects the history of sedimentary rock formation and changing life.

gradualism The idea that evolution progresses via slow, steady, gradual change; suggests that changes accumulate continuously as one species evolves to become another.

index fossils Widespread, short lived fossils that can be used to help identify rock layers of the same age spread around the Earth, providing the relative age of other fossils.

macroevolution Evolution at or above the species level.

microevolution Describes changes within a species or population.

molecular clocks Measure changes in DNA or proteins to indicate degrees of relationship among species.

paleontologists Scientists who study fossils.

punctuated equilibrium Proposes that species remain the same for long periods, and that change occurs infrequently but rather rapidly under unusual conditions such as geographic isolation or migration.

quantum evolution Proposes that the origins of major groups (families, orders, and classes) occurred as a response to drastic changes in environment or adaptive zones.

trace fossils Fossils consisting of footprints, burrows, droppings, eggs, nests, and other types of impressions.

Points to Consider

- Consider the range of tools used to study a history which no human could witness. These range from fossils – the actual remnants of living organisms – to comparisons of molecules within organisms still living today. Which tools do you consider most reliable? Does the fact that the information from one set of tools often confirms that evidence collected using a different set of tools strengthen your acceptance of the data?
- Review the various patterns of macroevolution, from mass extinction to coevolution and coextinction. Which of these best support the depiction of evolution as a bush, rather than an arrow? Which support the idea that evolution builds on what already exists, so the more variety there is, the more there can be in the future?

11.2 Lesson 11.2: Early Life

Lesson Objectives

- Relate the nature of science to our current understanding of the origin of life.
- Describe the formation of the atoms which build the Earth and its life.
- Explain the formation of the moon, and its effects on Earth's conditions for life.
- Compare and contrast Earth's early atmosphere with today's atmosphere.
- Discuss the formation of Earth's early atmosphere and oceans.
- Indicate the age of the Earth and identify supporting evidence.
- Interpret the importance of Miller and Urey's experiment.
- Relate the properties of phospholipids to the formation of the first membranes.
- Compare and contrast the "genes-first" model of the origin of life to the "metabolism first" model.
- Explain why some scientists believe that RNA was the basis of early life.
- Evaluate the hypothesis that exogenesis explains the origin of life on Earth.
- Describe the theoretical characteristics of the first cell.
- Discuss the concept of a "LUCA," or last universal common ancestor.
- Indicate the origin of photosynthesis and its consequences for Earth's life and atmosphere.
- Analyze the effects of the development of atmospheric oxygen on life.
- Explain the importance of the emergence of cellular respiration.

- Explain the Endosymbiotic Theory of the origin of eukaryotic cells.
- Evaluate the evidence for the Endosymbiotic Theory.
- Identify the origins of the three major domains of life.
- Analyze the evolutionary potential of the eukaryotic cell.
- Discuss the pros and cons of the evolutionary "tree" as a way of depicting the evolutionary process.

Introduction

No part of the story of life holds more mystery or fascination than its ultimate origins. Cosmologists, geologists, paleontologists, and biologists have collected, compared, scrutinized, evaluated, and revised many kinds of evidence in order to see into the past. As a result, well-accepted theories now illuminate nearly 4 billion years of life's history, 4.6 billion years of Earth's history, and even 13.7 billion years back to the **Big Bang**, which began the universe as we know it. Yet until the 19th century, most people believed the Earth was just 6,000 years old. We still do not know whether life exists beyond our Earth, nor can we predict where evolution will take life on Earth in the future, and our theories leave many chapters of the story untold. As you explore the early history of life, you must remember that the nature of science is to continue to question its own conclusions, to persist in seeking new information, and to readily modify or even overturn long-accepted theories, if new evidence contradicts them. This lesson includes some of the best explanations science can currently provide for life's origin and early evolution. A story of stardust, explosions, collisions, competition, and cooperation should not disappoint you, but it probably won't give you all the answers you seek. If this lesson provides insight and raises more questions, you will have a firm foundation upon which to build future understanding as it unfolds. Perhaps you could join the search!

Formation of Earth: We are Made of Stardust!

We will begin our story of the origin of life by exploring the origin of the materials which build it. The materials have a beauty and diversity of their own; perhaps your study of the Periodic Table of the Elements gave you an appreciation for their variety and individuality. Earth began as the solar system began – often described as a giant rotating cloud of dust, rocks, and gas. "Dust, rocks, and gas" may not sound inspiring, but this cloud contained the 92 elements or kinds of atoms which somehow combine to form every corner – living and nonliving - of the exquisite world we inhabit. The Big Bang (9 billion years earlier!) produced the atoms of hydrogen and helium. Elements as heavy as lithium followed the Big Bang within minutes. Stars such as red giants fused hydrogen and helium nuclei to form elements from carbon (the foundation of life!) to calcium (now our bones and teeth). Supernova explosions formed and ejected heavier elements such as iron (for red blood cells). We are not just "dust." We - and our world - are stardust!

How did this rotating cloud of stardust become our solar system? One theory suggests that a nearby supernova sent a shock wave through the cloud, increasing its spin to form a protoplanetary disk, shown in **Figure** 11.19. Most of the mass concentrated in the middle and began to heat up, but large debris and collisions resulted in concentrations of matter outside the center. Eventually, heat in the central core began nuclear fusion of hydrogen to helium, and the Sun ignited. Matter outside the Sun's gravity separated into rings of debris, and collisions of objects within the rings formed larger objects, which eventually became the planets. Solar wind cleared much of the remaining non-planetary material from the disk.

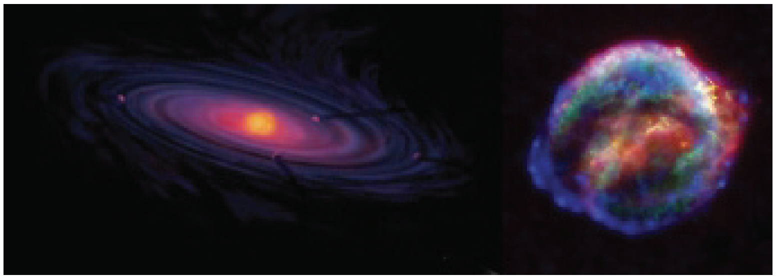

Figure 11.19: At left is an artist's conception of the protoplanetary disk, which eventually formed our solar system. At right is an X-ray image of the remnant of Kepler's Supernova, SN 1604, constructed of images from NASA telescopes and observatories. Together, art and science suggest the beauty of the "dust, gas, and rocks" which gave birth to our earth and its life. (40)

One of the collections of debris, approximately 150 million kilometers from the Sun, was the protoplanet Earth. Newborn, Earth was very different from the home we know today. Bombarded by debris and heated by radioactive decay and the pressure of contraction, the Earth at first was molten. Heavy elements sank to the center, and lighter ones surfaced. Heat and solar wind meant that no atmosphere and no oceans were present.

Eventually, contraction and cooling allowed formation of a crust and retention of an atmosphere. However, continued bombardment melted portions of the crust for long periods. About 4.5 billion years ago, Earth collided with another protoplanet, Theia. This "big whack" gave us our moon and tilted Earth on its current axis, leading to the seasons, which now influence so much of life's diversity. The Big Whack may also have initiated plate tectonic activity by speeding up the Earth's rotation. Since then, however, the moon's tidal drag may be slowing that rotation; scientists suggest that the day/night cycle during the Hadean may have been as short as 10 hours.

As the Earth continued to cool amidst heavy bombardment, steam escaped from the crust and active volcanoes released other gases to form a primitive atmosphere, which contained ammonia, methane, water vapor, carbon dioxide, and nitrogen, but no more than a trace of oxygen. In the absence of oxygen, no ozone layer protected Earth from the Sun's ultraviolet rays. Between 4.2 and 3.8 billion years ago, clouds and rain formed the oceans. The oceans were olive green, and the reddish atmosphere would have been toxic to modern multicellular organisms. Yet the stage was set for life to begin.

First Organic Molecules: Hypotheses About the Origin of Life's Chemistry

The Hadean Eon ended 3.8 billion years ago, its timeline marked by Earth's oldest known rocks (between 3.8 and 4.2 billion years old) and oldest known minerals (formed 4.4 billion years ago). Scientists use these dates to estimate that the Earth itself is 4.6 billion years old. Evidence for life during the Hadean does not exist, although many scientists push the theoretical origin back that far. How – and when – did life arise?

Once again, we will begin with the materials of life – this time, **organic molecules,** made primarily of the element carbon. Most scientists agree that these organic molecules arose before cells, which we now consider essential to the definition of life. Several hypotheses and experiments suggest ways in which organic building blocks may have formed.

In 1924, Aleksandr Oparin proposed that life could have developed through gradual chemical evolution in a "**primordial soup**." In 1953, Stanley Miller and Harold Urey designed a now-famous test of the hypothesis that the conditions of primitive Earth favored chemical reactions that synthesized organic molecules from inorganic precursors. Their experiment (**Figure** 11.20) showed that a mixture of gases, believed to be part of the primitive Earth atmosphere, when subjected to sparks representing lightning, formed a mixture of monomers representing each of the four major groups of organic molecules. Although DNA, RNA, and polymers were absent, 13 of the 22 amino acids that make up modern protein, plus lipids, sugars, and some building blocks of DNA and RNA, were among the products of the experiment.

The "leap" from building blocks to polymers and from organic soup to individual replicating units has been more difficult to demonstrate. In the '50s and '60s, Sydney Fox showed that early Earth conditions could result in short chains of amino acids, which in turn could form enclosed spheres. Phospholipids can self-organize into membranes in a similar fashion, and cell membranes today consist primarily of a bi-layer of these lipids. Phospholipids or polypeptides could have surrounded and protected early metabolic units, forming **protocells** shown in **Figure** 11.21, simple membrane-enclosed spaces which may have led to the later evolution of true cells.

Walter Gilbert, Carl Woese, and Alexander Rich proposed that RNA, because it can serve both catalytic and replicating functions, was the first informational molecule, and formed the "**RNA World Hypothesis**" for the origin of life. Sol Spiegelman created a short chain of RNA which was able to replicate itself in the presence of RNA polymerase; the segment is now known as the "Spiegelman monster." The idea that a successful replicator molecule preceded the evolution of biochemical pathways is the "**Genes-First**" model.

In contrast, Günter Wächtershäuser proposed that sulfides of iron and other minerals con-

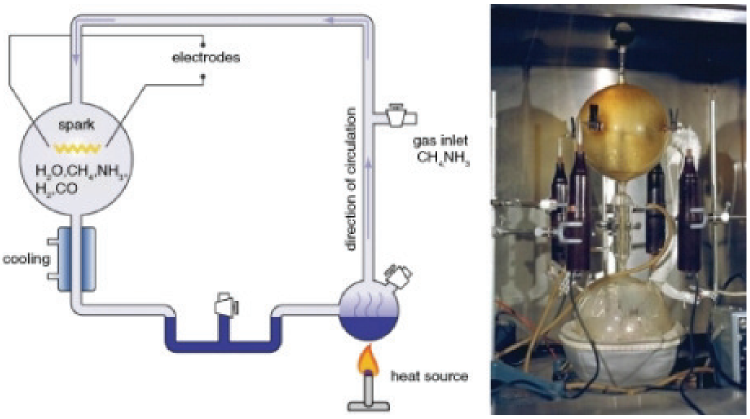

Figure 11.20: The Miller-Urey experiment subjected a mixture of gases thought to be present in Earth's primitive atmosphere to sparking, representing lightning. After one week, the nonliving system had formed 13 of the 22 amino acids which make up modern proteins, sugars, lipids, and some of the building blocks of DNA and RNA. (32)

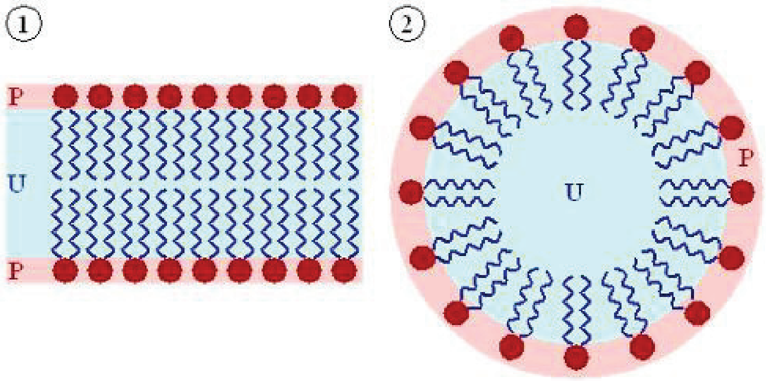

Figure 11.21: Phospholipids, with hydrophilic phosphate "heads" (P) and hydrophobic lipid "tails" (L) self-assemble into membranes (1) and enclosing spheres (2) which could have protected early metabolism from "outside" chemical disturbances. (29)

tain energy which could have polymerized basic building blocks. He argued that extensive evolution of biochemical pathways might have preceded replicator molecules and individualization of life. His ideas formed the basis of William Martin and Michael Russell's 2002 hypothesis that black smokers at seafloor spreading zones, shown in **Figure** 11.22, could have provided conditions for extensive chemical and biochemical pathway evolution. Their reasoning suggests that lipid membranes allowing independent lives away from the smokers could have been a last step in early evolution. The fact that archaebacteria and eubacteria (and us eukaryotes!) have completely different membrane lipids but similar metabolism supports the concept of early biochemical pathway evolution. These ideas comprise the "**Metabolism-First**" model.

The discovery of organic molecules in space supports the **exogenesis** hypotheses which propose that life could have originated elsewhere – on Mars, or at some distant point in the universe. Comets and meteorites are known to contain organic molecules, and could have delivered them to Earth. Exogenesis does not really answer the question of how life originated, but provides a much wider temporal and spatial framework in which it could have happened.

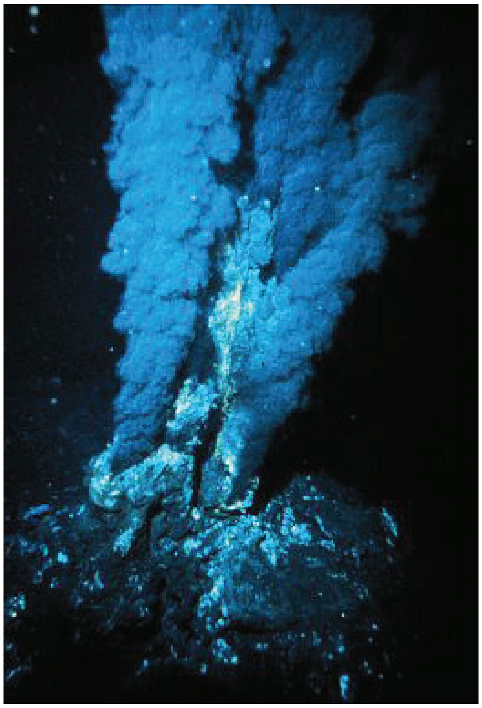

Figure 11.22: Black smokers at a mid-ocean ridge hydrothermal vents could have provided conditions suitable for the evolution of early biochemical pathways and much of metabolism, even before lipid membranes formed cells. Martin and Russell propose that the last universal common ancestor may have emerged from a black smoker. (25)

Emergence of Life: The First Cells were Prokaryotes

Although many hypotheses and some experiments and observations explore the origin of cellular life, actual events remain unknown. If earth's life first arose on earth, rather than by exogenesis, its timing is speculative, for no fossils record that event. Admitting that many conflicting hypotheses exist, we often express our current understanding of the story this way:

Perhaps four billion years ago during the Hadean Eon, lightning and a primitive atmosphere produced an organic soup of chemicals. As the "soup" became more concentrated, molecules began to interact with one another. As molecules became more complex, some molecules helped to speed up or catalyze chemical reactions (perhaps RNA, but eventually protein). Within that highly reactive soup, a molecule gained the ability to copy itself, becoming the first replicator (perhaps RNA, but eventually DNA). Copies contained errors, and errors which prevented replication caused the copies to "die out." Copies that replicated faster survived to make more copies. Eventually, lipid membranes surrounded some of these chemicals, protecting them from reacting with other chemicals.

Although many protocell "species" probably populated the early "soup," scientists believe that only one – a last universal common ancestor (**LUCA**) – emerged about 3.5 billion years ago during the Archean Eon, and later gave rise to all cellular life on earth. This **prokaryote** probably had a cell membrane and ribosomes, and used DNA for information storage, RNA for information transfer, and protein for catalyzing chemical reactions – like all life today. The first cells were probably **heterotrophs**, feeding on energy-rich chemicals concentrated in the "soup." Alternatively, they could have been **chemoautotrophs**, extracting energy from inorganic molecules. Not long after prokaryotic cells emerged, they split into two major groups, Eubacteria and Archaebacteria. Both persist today, although Archaebacteria more often inhabit extreme habitats.

Inevitably, a diminishing supply of food molecules led to competition. At some point, **glycolysis** evolved as a pathway for transferring energy from organic molecules to ATP. This pathway persists in almost all organisms today.

Eventually, about three billion years ago, a new strategy evolved among some prokaryotes, which used sunlight to make carbohydrates from carbon dioxide and water. **Photosynthesis** provided a new source of food molecules for both autotrophs and the heterotrophs that "learned" to consume them. The oldest fossils, stromatolites, (**Figure** 11.23) record abundant photosynthetic cyanobacteria from that time.

Oxygen produced by photosynthesis first oxidized iron dissolved in the oceans, creating massive deposits of iron ore. Eventually, toward the end of the Archean, oxygen began to accumulate in the atmosphere, creating a major environmental change that is sometimes called the "**Oxygen Catastrophe**." Oxygen was indeed toxic to many of the prokaryotes which had evolved as **anaerobes**. However, ultraviolet rays converted some of the oxygen to ozone, which prevented much of that harmful radiation from reaching the earth's surface.

Figure 11.23: Stromatolites are microbial mats made by some of the earliest photosynthetic organisms on Earth. Fossil stromatolites (left) are among the oldest fossils on Earth, although some have been interpreted to be of abiotic origin. Living stromatolites (right), mats of cyanobacteria, are found primarily in hypersaline lakes and marine lagoons. (36)

Thus, while an oxygen atmosphere may have killed many species, it allowed survivors to colonize previously uninhabitable ocean surface and terrestrial habitats. Even more important to the future of life, some prokaryote survivors "learned" how to use oxygen to harvest a great deal more energy from organic molecules. The energy efficiency of **aerobic respiration** paved the way for the emergence of larger and more complex organisms in the Proterozoic Eon.

Eukaryotes: Alliance, Invasion, or Slavery?

You have learned that our own **eukaryotic** cells protect DNA in chromosomes with a nuclear membrane, make ATP with mitochondria, move with flagella (in the case of sperm cells), and feed on cells which make our food with chloroplasts. All multicellular organisms and the unicellular Protists share this cellular intricacy. Bacterial (prokaryotic) cells are orders of magnitude smaller and have none of this complexity. What quantum leap in evolution created this vast chasm of difference?

The widely accepted **Endosymbiotic Theory**, shown in **Figure** 11.24, proposes that many organelles were once independently living cells. Larger cells engulfed these smaller cells but did not digest them, perhaps due to prey defenses. Alternatively, perhaps the smaller cells invaded the larger cells with the "intent" to parasitize. In either case, with their own DNA, the endosymbionts reproduced independently within the cell, and cell division passed them on to future generations of cells. Aerobic bacterial invaders would have been able to use oxygen to further break down and use energy from the host's "wastes" from glycolysis. So much energy (ATP) resulted that some was available to the host; a mutually beneficial symbiosis resulted. This intriguing story of cooperation – so different from natural selection's emphasis on competition – explains the origin of our mitochondria. A similar tale is told for chloroplasts; the benefit for a heterotrophic "host" is clear. Some scientists view cilia, flagella, peroxisomes, and even the cell nucleus as endosymbionts, but these ideas are less widely accepted.

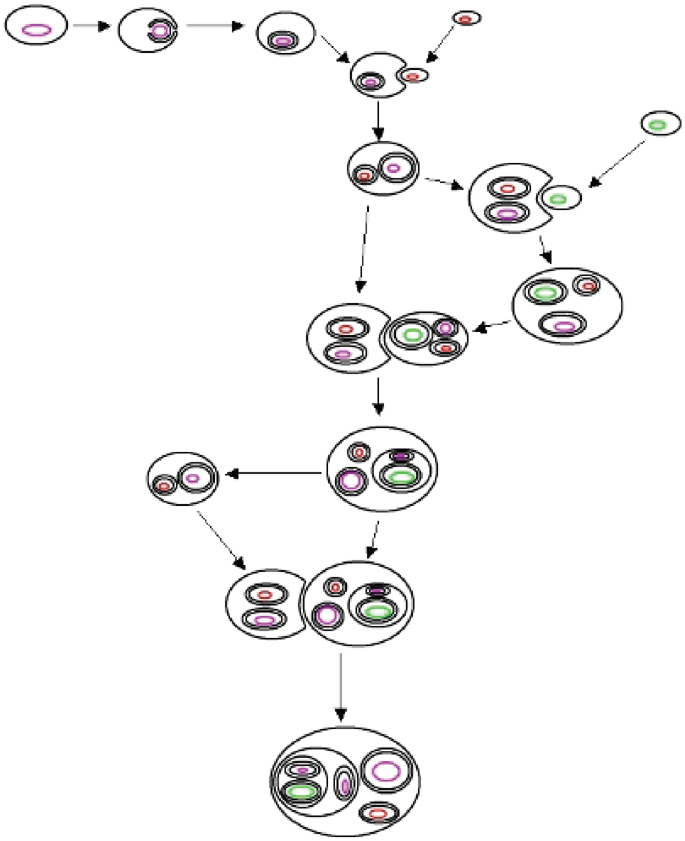

Figure 11.24: The Endosymbiotic Theory holds that eukaryotic cells arose when larger prokaryotic cells engulfed smaller, specialized prokaryotes, without later digestion. The smaller cells reproduce independently within the larger cells, to the potential benefit of both. The diagram shows possible events leading to endosymbiosis. Black: membrane; Pink: eukaryotic DNA; Green: cyanobacteria/chloroplast DNA; Red: proteobacteria/mitochondrial DNA (8)

What is the evidence for this maverick evolutionary pathway? Biochemistry and electron microscopy provide convincing support for the Endosymbiotic Theory. The mitochondria and chloroplasts which live within our eukaryotic cells share the following features with prokaryotic cells:

- Organelle DNA is short and circular – and sequences do not match DNA in the nucleus.
- Molecules that make up organelle membranes resemble those in prokaryotic membranes – and differ from those in eukaryotic membranes.
- Ribosomes in these organelles are similar to those of bacteria – and different from eukaryotic ribosomes.
- Reproduction is by binary fission – not mitosis.
- Biochemical pathways and structure show closer relationships to prokaryotes.
- Two or more membranes surround these organelles.

The "host" cell membrane and biochemistry are more similar to those of Archaebacteria, so scientists believe eukaryotes descended more directly from that major group (**Figure** 11.25). However, the standard evolutionary tree cannot accurately depict our ancestry, because the origin of the eukaryotes combines traditional descent from the Archaea with landmark cohabitation alliances forged with the Bacteria.

The timing of this dramatic evolutionary event (more likely a series of events) is not clear. The oldest fossil clearly related to modern eukaryotes is a red alga dating back to 1.2 billion years ago. However, many scientists place the appearance of eukaryotic cells at about 2 billion years. Some time within Proterozoic Eon, then, all three major groups of life – Bacteria, Archaea, and Eukaryotes – became well established. Geologists hypothesize the oldest supercontinent, Columbia, between 1.8 and 1.5 years ago, as the backdrop for the further evolution of these three domains.

Eukaryotic cells, made possible by endosymbiosis, were powerful and efficient. That power and efficiency gave them the potential to evolve new ideas: multicellularity, cell specialization, and large size. They were the key to the spectacular diversity of animals, plants, and fungi which populate our world today. We will tell their much more familiar story in the next lesson. Nevertheless, as we close the history of early life, reflect once more on the remarkable but often unsung patterns and processes of early evolution. Our "size-ism" sets us up to wonder at plants and animals, and ignore bacteria. Our human senses cannot directly perceive the unimaginable variety of single cells, the architecture of organic molecules, or the intricacy of biochemical pathways. Let your study of early evolution give you a new perspective – a window into the beauty and diversity of unseen worlds – now and throughout Earth's history. Apart from the innumerable mitochondria which call your 100 trillion cells home, your body contains more bacterial cells than human cells. You, mitochondria, and your resident bacteria share common ancestry – a continuous history of the gift of life.

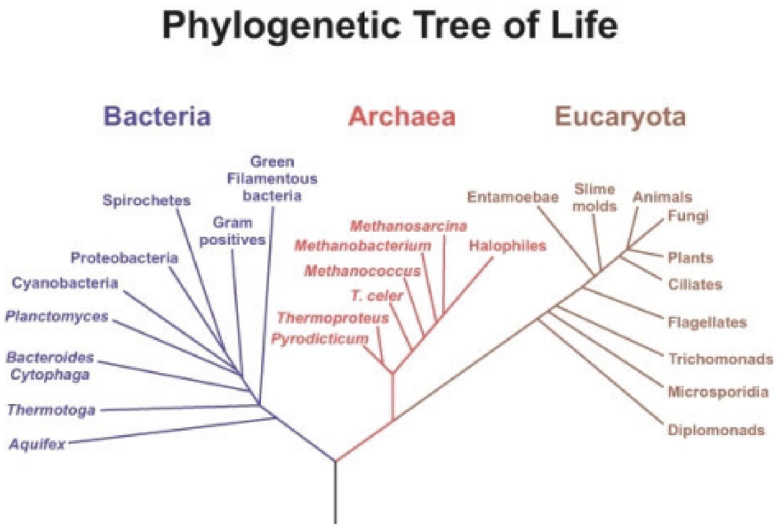

Figure 11.25: The three major domains of life had evolved by 1.5 billion years ago. Biochemical similarities show that we Eukaryotes share more recent common ancestors with the Archaea, but our organelles probably descended from Bacteria by Endosymbiosis. (48)

Lesson Summary

- The Big Bang and stars such as red giants made the atoms which build life.
- Earth gradually condensed into a molten protoplanet, constantly bombarded with debris.
- Steam escaping from the formative crust and volcanic gases contributed to Earth's early atmosphere, which probably contained methane, ammonia, carbon dioxide, water and nitrogen. Such an atmosphere would be toxic to most modern organisms.
- No oxygen meant no ozone; ultraviolet radiation reached the Earth and threatened life with deadly, mutating rays.
- Eventually, water in the atmosphere condensed into clouds and rain, forming oceans.
- Earth's oldest known rocks are between 3.8 and 4.2 billion years old. The oldest minerals are 4.4 billion years old. Scientists estimate that the age of the Earth is 4.6 billion years.
- Miller and Urey showed that a spark igniting a mixture of gases resembling Earth's primitive atmosphere could produce most of the building block organic molecules of life – forming an "organic soup."
- Some lipids and certain polypeptides can spontaneously form into protocells; early membranes could have self-organized in this way.
- The "Genes-first" hypothesis proposes that replicating molecules evolved before biochemical pathways.
- Some scientists believe RNA, rather than DNA, was the first replicator.
- The "metabolism-first" model suggests that biochemical pathways evolved in an or-

ganic soup before self-replicating molecules.
- Many scientists accept that a "last universal common ancestor" (LUCA) cell arose from the primeval soup of organic molecules.
- This prokaryote probably had a cell membrane and ribosomes, and used DNA for information storage, RNA for information transfer, and protein for catalyzing chemical reactions – like all life today.
- The first cells were probably heterotrophs feeding on organic soup, or chemoautotrophs using the energy in inorganic molecules.
- Not long after the LUCA prokaryote arose, life split into two groups, Bacteria and the Archaebacteria.
- Photosynthesis arose roughly 3 billion years ago.
- The oldest fossils, stromatolites, preserve photosynthetic cyanobacteria.
- Oxygen produced by photosynthesis eventually changed Earth's atmosphere.
- Ozone formed, protecting life from damaging UV radiation.
- The widely accepted Endosymbiotic Theory explains the origin of eukaryotic cells as a merging of several kinds of prokaryotic cells.

Review Questions

1. Why is understanding the nature of science important to studying the origin of life on Earth?
2. Interpret the statement "we are made of stardust."
3. Describe the effects of the moon on the conditions for life on Earth, according to the impact theory of the moon's origin.
4. Discuss the formation of Earth's atmosphere and compare it to today's.
5. Identify the age of the Earth, and give the supporting evidence.
6. Describe Miller and Urey's experiment, and evaluate its importance to our understanding of the origin of life.
7. Compare and contrast the RNA World, genes first, metabolism first, and exogenesis models of the origin of life. Evaluate the evidence supporting each model.
8. List the characteristics scientists attribute to "last universal common ancestor" of life on Earth.
9. Indicate when scientists believe photosynthesis originated, and what evidence suggests this. Analyze the effects of the origin of photosynthesis on life existing at that time.
10. Analyze the theory which explains our current understanding of the origin of eukaryotic cells. In what way does it differ significantly from "traditional" ideas of evolution?

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Vocabulary

endosymbiotic theory Theory which proposes that many organelles were once independently living cells; describes the formation of eukaryotic cells.

genes-first model The idea that a successful replicator molecule preceded the evolution of biochemical pathways.

LUCA The last universal common ancestor; the first true cell, which formed about 3.5 billion years ago.

metabolism-first model The proposal that extensive evolution of biochemical pathways might have preceded replicator molecules and individualization of life.

organic molecules The “materials of life” - molecules made primarily of the element carbon.

oxygen catastrophe Toward the end of the Archean, oxygen began to accumulate in the atmosphere, killing many anaerobic species.

primeval soup Oceans in which gradual chemical evolution formed life; proposed by Aleksandr Oparin.

protocells Simple, membrane enclosed early metabolic units surrounded by phospholipids or polypeptides; precursors to true cells.

RNA world hypothesis Hypothesis that proposes that RNA evolved prior to DNA.

Points to Consider

- Which theory of life’s origins do you consider most plausible: genes first, metabolism first, or exogenesis? What kinds of evidence would be required to support each theory?
- The standard form for an evolutionary tree is a series of branching lines which show common ancestors. Can you imagine a format which could show Endosymbiosis, as well as common ancestry?

11.3 Lesson 11.3: Multicellular Life

Lesson Objectives

- Assess the impact of global environmental changes on the evolution of life.
- Describe the diversity of unicellular organisms which arose over 2 billion years of evolution.
- Evaluate the importance of major evolutionary developments which preceded the Cambrian explosion: colony formation, cell specialization, and sexual reproduction.
- Evaluate the importance of some factors which contributed to the “Cambrian explosion” of biodiversity.
- Trace the evolution of plants and animals from aquatic to terrestrial habitats.
- Connect changes in atmospheric O_2 and CO_2, temperature, geography, and sea level to extinctions and radiations of various groups throughout the Paleozoic.
- Identify recurrent extinctions as losses of diversity, but also opportunities for the evolution of new species.
- Describe the conditions under which the dinosaurs emerged to dominate life on Earth.

- Identify the diversity of habitats and niches occupied by the dinosaurs during their "golden age."
- Discuss the relationships between reptiles, birds and mammals during the age of the dinosaurs.
- Explain the coevolution of flowering plants and insects during the Cretaceous.
- Evaluate the evidence for an "impact event" as the primary cause of the K-T extinction which ended the reign of the dinosaurs.
- Analyze the emergence of mammals and birds as the dominant land animals during the early years of the Cenozoic.
- Connect sea level, land bridges, and climate to their effects on evolution.
- Explain the connection between CO_2 levels, temperature, and glaciation.
- Discuss the factors which contribute to the "sixth" major extinction.

Introduction

Biologists estimate that 99% of the species which have ever lived on Earth are now extinct, and up to 80 million species populate our world today. It is the great diversity of species that allows at least some organisms to survive major changes in the environment.

4 billion years of simple, prokaryotic cells

3 billion years of photosynthesis

2 billion years of complex, eukaryotic (but still single!) cells

1 billion years of multicellular life

The history of life reaches the last billion years of Earth's 4.6 billion-year history with no hint of the wondrous diversity of life as humans know it. Not until nearly 80% of Earth's history had passed did multicellular life evolve. The fossil record tells the story: millions of species of fish, amphibians, reptiles, birds, mammals, mosses, ferns, conifers, flowering plants, and fungi populated the seas and covered the Earth - as continents crashed together and broke apart, glaciers advanced and retreated, and meteors struck, causing massive extinctions. Life has had a colorful and exciting last billion years, spawning diversity almost beyond our comprehension.

And yet, the giant steps of evolution remain back in the Precambrian. Its catalog of evolutionary innovations is long and impressive:

- Energized elements from stardust formed simple organic molecules.
- Building blocks chained together to form catalysts and self-replicating macromolecules.
- Biochemical pathways evolved.
- Protective yet permeable membranes enclosed the catalysts, replicators and their metabolic retinue.
- Early prokaryotic cells "learned" to make ATP by splitting glucose.

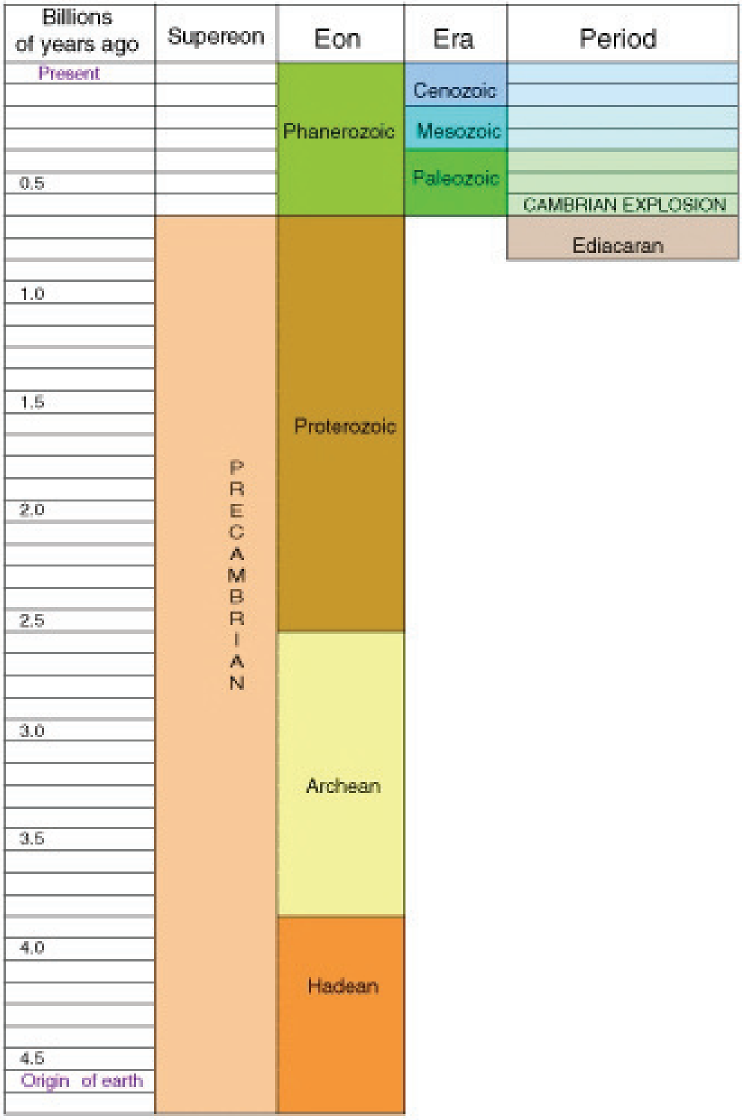

Figure 11.26: (9)

- Others began to harvest sunlight energy through photosynthesis.
- Photosynthetic cyanobacteria produced vast amounts of “waste” oxygen, dramatically altering the Earth’s atmosphere.
- The oceans rusted (iron ore deposits).
- An ozone layer formed, shielding life from UV radiation.
- The “O_2 catastrophe” killed many anaerobic prokaryotes.
- Still other prokaryotes “learned” to use the new O_2 to release the energy remaining in carbohydrates products of glycolysis.
- Endosymbiosis created eukaryotes, firmly establishing the three major evolutionary lineages, which yet today comprise the living world.

The timing and exact nature of most of these innovations is speculative; indeed, the first few may have been extraterrestrial and even deeper in time. They comprise perhaps the most important landmarks in the evolution of life, but the fossil record is sketchy due to prokaryote size, rock layer metamorphosis, and burial by more recent rocks.

Overall, we know remarkably little about Precambrian life. The **Cambrian Period** documents the greatest flowering of life of all time, and gives its name - in a rather negative sense - to the 4 billion years of Earth history that preceded it. Before we dive into the famous Cambrian “explosion,” we will look more carefully at the last Eon of the Precambrian, which set the stage for this most famous burst of evolution.

Late Precambrian: Setting the Stage for an Explosion of Biodiversity

The geologic record of the Proterozoic, the most recent eon of the Precambrian, is much better than that of the Archean and Hadean Eons before it. Accordingly, we know that **supercontinents** formed by collision and broke apart by rifting. The atmosphere changed dramatically with the addition of oxygen and a protective ozone layer. Glaciations covered much of the Earth with ice so extensively that it is known as the **“Snowball Earth”** during that period (**Figure** 11.27). Eventually, enough CO_2 escaped from volcanoes to begin a period of global warming; melting opened a great variety of new niches. The severe restriction and subsequent opening of opportunities may have driven the later Cambrian explosion.

Within this dramatic environmental panorama, the three major lineages of life – Bacteria, Archaea, and Eukaryotes continued to diversify. Plant, animal, and fungal ancestors diverged as solitary cells. Gradually, some of these cells began to live in colonies. Within the colonies, primitive **specialization** among cells made certain tasks more efficient. The modern green alga, *Volvox* illustrates a comparable level of organization (**Figure** 11.28). The line between colonies and multicellular organisms is difficult to draw, but most scientists agree that true plants had evolved by about 1 billion years ago, and animals evolved about 100 million years later.

Figure 11.27: The geologic record documents at least two ice ages during the last eon of the Precambrian. One was so severe that some scientists believe ice then covered the entire globe, and they dub it the "Snowball Earth." The icy constriction of life and later meltdown opening of niches may have contributed to the explosive evolution of the Ediacaran and Cambrian Periods that followed. (24)

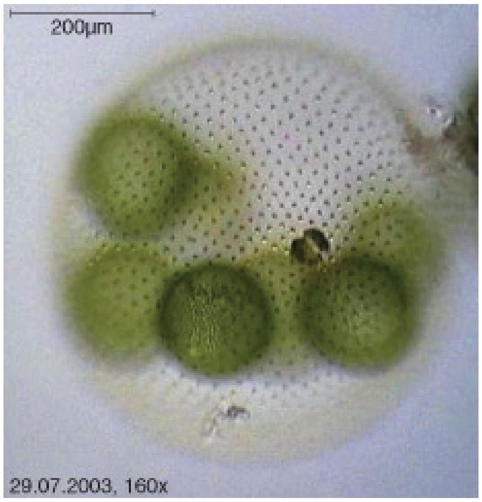

Figure 11.28: The green alga *Volvox* shows the multicellularity and early cell specialization which probably characterized early colonial eukaryotes. Specializations include anterior sensory cells, asexual and two types of sexual reproductive cells, and coordination among flagellate cells. (50)

The fossil record shows that some eukaryotes had begun to reproduce sexually by a little over a billion years ago (**Figure** 11.29). **Sexual reproduction** was a major evolutionary innovation, producing more variety among offspring and thus more rapid adaptation to changing environments.

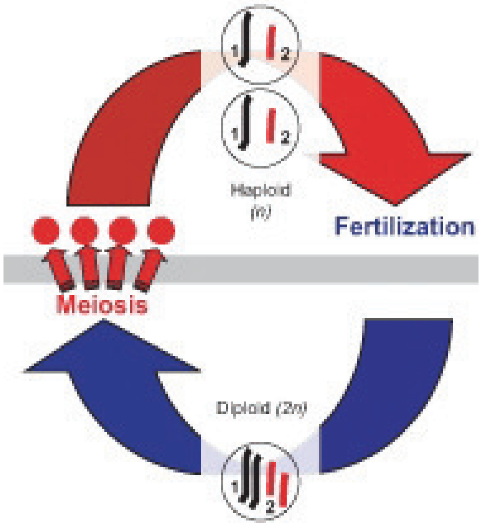

Figure 11.29: The evolution of sexual reproduction around 1 billion years ago increased variety among offspring, and may have increased rates of evolution (see *Cell Division and Reproduction* chapter). (45)

Near the end of the Precambrian - not until just over 600 million years ago, a unique assemblage of multicellular organisms left a fossil record which gives us our first glimpse of multicellular diversity – the **Ediacaran biota** (the name is taken from the hills in Australia where the first such fossils were found) (**Figure** 11.30).

Members of this community include:

- some familiar organisms such as sponges, red and green algae, and bacteria
- very few ancestors of modern animals
- many unique disk, bag, and quilt like animals which do not resemble any modern animals

The origin and relatively rapid extinction of this entire group remain somewhat of a mystery. The oxygen atmosphere and/or an ice age may explain their initial radiation. Their abrupt and nearly complete disappearance may have resulted from unbalanced predation, grazing, or competition, or yet another environmental crisis such as supercontinent breakup, changes in ocean chemistry, and/or rising sea levels. Whatever the causes, most species disappeared by the end of the Precambrian, about 542 million years ago. The Ediacarans appear to have been an early multicellular, dead-end branch on the bush of life. Their extinction, however,

Figure 11.30: *Spriggina* (top), an Ediacaran fossil, may be an ancestor of the trilobites. *Charnia* (bottom), the first accepted complex Precambrian organism, is more typical of the Ediacaran biota – it is difficult to show relationships to any modern species. (22)

appears to have paved the way for a spectacular evolution of much more familiar life, which marks the beginning of the modern Phanerozoic Eon: the Cambrian explosion.

Paleozoic Era: Ancient Plants and Animals, but Seeds of Modern Life

Figure 11.31: (43)

The Paleozoic era of the current, Phanerozoic Eon is the first concrete chapter of life's history (**Figure** 11.31). Abundant fossils, clearly related to modern animals, plants and fungi, illuminate the path of evolution beginning with its first Period, the Cambrian, 542 million years ago. However, the sudden appearance of such variety presents yet another puzzle in the story of life: how did roughly 50 major groups of organisms evolve so rapidly, without apparent ancestors? The abrupt emergence of so many phyla has given this period in geologic time its nickname, the **Cambrian explosion**, but its causes remain hypothetical. As for the Ediacaran radiation, major environmental changes have been proposed but not convincingly documented. A major geologic event of the Paleozoic is the amalgamation of the supercontinent Gondwana, but it does not seem to explain the extent of the increase in Cambrian diversity. Perhaps life itself was responsible: a "critical mass" of development could have opened up new body pattern options, or more kinds of life opened more kinds of ecological niches. Whatever the cause, the evidence shows that nearly all modern animal phyla, including our own chordate phylum, are represented in this diversity of life. Among the most common and famous are reef-building sponges and arthropods, known as **trilobites** (**Figure** 11.32). Both were diverse and abundant during the Cambrian but later became extinct. However, the phyla they represent persist today.

Figure 11.32: Two representatives of more than fifty modern animal phyla from the Cambrian explosion are reef-building sponges (left) and early arthropods known as trilobites (right). Both were abundant during the Cambrian and later became extinct; however, the phyla they represent persist to this day. (11)

A major extinction marks the boundary between the Cambrian and **Ordovician Periods** 488 million years ago (**Figure** 11.33). In warm, shallow continental seas, Ordovician life rebounded:

- A great diversity of new invertebrates swam the seas.
- **Liverworts** may have been the first green plants to appear on land (**Figure** 11.34).
- The first fish, jawless and bony-plated ostracoderms, swam slowly along shallow sea bottoms.

About 444 million years ago, a sharp drop in atmospheric CO_2 led to glaciation and ended the long stable period of warm seas. The Ice Age affected marine genera severely; up to 60% disappeared! This major extinction marks the end of the Ordovician and the beginning of the **Silurian Period**.

Figure 11.33: An artist's rendition shows that the second period of the Paleozoic, the Ordovician, heralded a great diversity of invertebrates, including nautiloids, crinoids, and bivalves. (28)

Figure 11.34: Among the first true plants, liverworts colonized the land during the Ordovician. Without vascular tissue, they were small and grew flat and low to the ground (right). Like all plants and nearly all eukaryotes, they had adopted sexual reproduction (left, female reproductive organ). Both photos are greatly magnified. (47)

During the Silurian, the glaciers retreated. Melting icecaps raised sea level, yet a new supercontinent, Euramerica, formed near the equator. In a long, stable greenhouse phase, warm shallow seas covered extensive equatorial landmasses, opening tropical habitats on land and in water:

- Reef-building corals and sea-scorpions evolved.
- The first jawed fishes joined armored jawless fishes and many invertebrates.
- Vascular plants solved the problem of carrying water into the air.
- Arthropods such as millipedes followed the plants onto land.

The Silurian ended about 416 million years ago with a minor extinction, which may have been due to an asteroid impact or increasing glaciation.

During the **Devonian Period**, terrestrial life expanded to include forests of clubmosses, horsetails, ferns, and the earliest seed-bearing plants and trees (**Figure** 11.35).

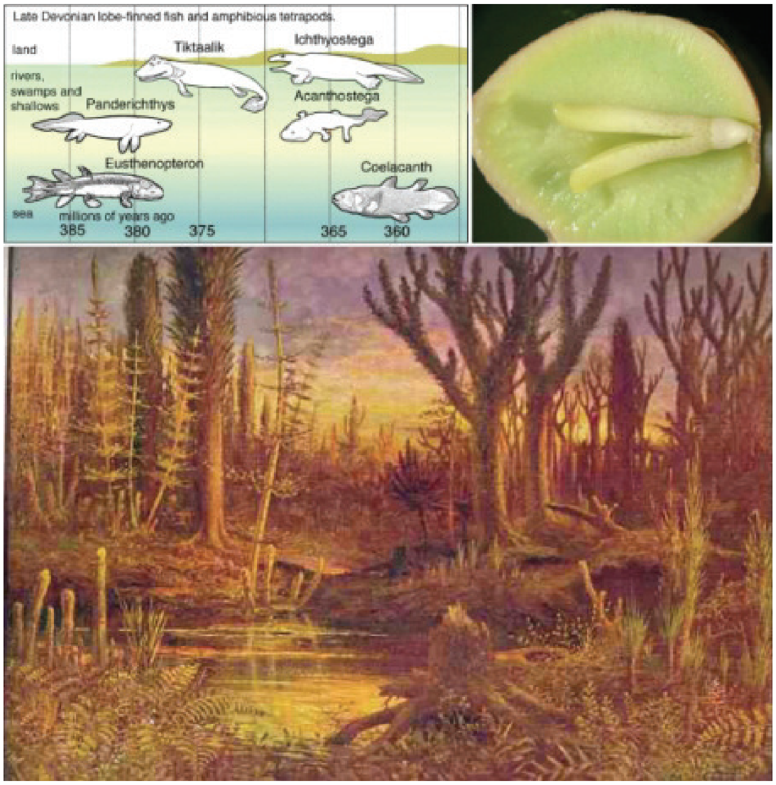

Figure 11.35: Devonian fish (above, left) evolved lobes which eventually allowed vertebrates to move to land. On land (below), clubmosses, horsetails, and ferns joined primitive seed plants and early trees to form the first forests. Seeds (above, right) allowed reproduction on dry land. (15)

- Seeds allowed plants reproduce on dry land in the same way that shelled eggs would later help animals. Insects appeared, although they were wingless at first.
- Squid-like animals and ammonite mollusks became abundant.
- Lobe-like fins allowed some fish to lift their heads above water and breathe air in oxygen-poor waters.

About 360 million years ago, extinction struck over 20% of marine families and over 50% of all genera, ending the Devonian. One hypothesis suggests that the greening of the continents absorbed CO_2 from the atmosphere, reducing the greenhouse effect and lowering temperatures.

Extensive coal deposits, fuel for our Industrial Revolution, characterize rocks of the **Carboniferous Period** which followed. Coal developed from new bark-bearing trees in widespread lowland swamps and forests. Fallen trees were buried without decaying – perhaps because animals and bacteria had not yet evolved digestive enzymes that could break down the new molecule, lignin, in the wood. Burial of carbon lead to a corresponding buildup of oxygen in the atmosphere; O_2 at the time was an all-time high of 35% (compared to 21% today). Abundant oxygen probably encouraged evolution, especially on land.

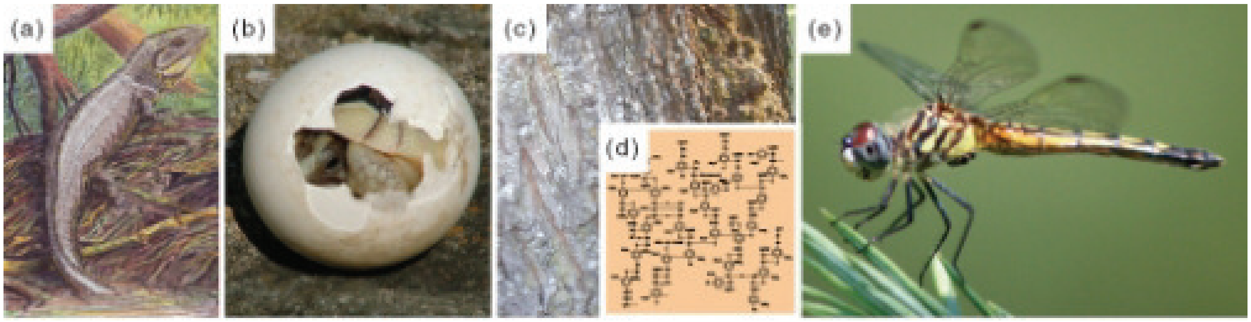

Figure 11.36: Vertebrates moved to land during the Carboniferous, and amphibians became abundant. Early lizards (A) were able to move to drier land in part because their new, shelled egg (B) did not dry out. Trees in widespread swamps evolved bark (C) containing as-yet non-biodegradable lignin (D), leading to the eventual formation of the coal which fueled our Industrial Revolution. With the highest known levels of O_2, giant insects such as dragonflies (E) flew the skies. (7)

As illustrated in **Figure** 11.36:

- Giant insects took to the air.
- Vertebrates moved to land; amphibians were far larger and more abundant and diverse than today.
- The shelled egg allowed early reptiles to reproduce on land without drying out the embryo.

- Early gymnosperms, reproducing with pollen rather than sperm, colonized dry land.

Toward the end of the Carboniferous, the climate cooled. Glaciation and extinction mark the border between the Carboniferous and the last period of the Paleozoic Era, about 300 million years ago.

The **Permian** is best known for the dramatic event which ended not only the period but also the entire Paleozoic Era – an extinction of 95% of the then-living world. If we look more closely at the effects of continental geography on climate, perhaps we can begin to understand not only that massive extinction, but also the major events in evolution which preceded it. During the Permian, all the major landmasses of earth combined into a single supercontinent, known as **Pangaea** (**Figure** 11.37). As for today's continents, much of the interior would have been dry with seasons of temperature change, because the oceans' moderating effects were too distant. Pangaea's size may have exaggerated this continental climate of seasons and drought. Three major groups of animals and plants evolved in response to Pangaea's extensive arid niches.

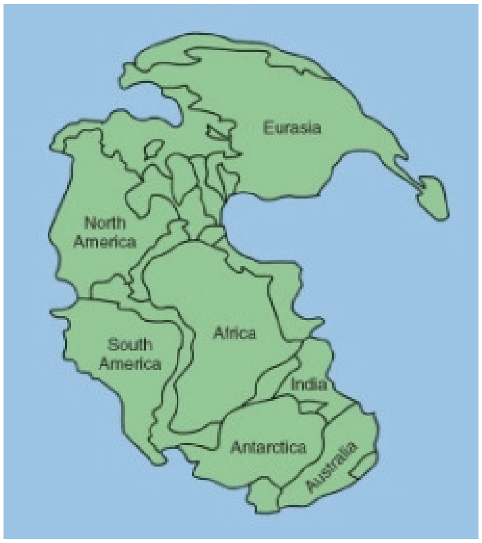

Figure 11.37: The supercontinent Pangaea encompassed all of today's continents in a single land mass. This configuration limited shallow coastal areas which harbor marine species, and may have contributed to the dramatic event which ended the Permian - the most massive extinction ever recorded. (38)

- Reptiles, with claws, scaly skin, and shelled eggs, diversified, foreshadowing Mesozoic dinosaurs.
- Cycads and other gymnosperms, with cuticle-covered leaves to limit water loss and cones to bear seeds, dominated forests.
- Insects evolved entire life cycles on dry land; beetles and flies navigated land and air.

At the end of the Permian, an estimated 99.5% of individual organisms perished. Several factors may have contributed, and one factor relates again to Pangaea. Marine biodiversity is greatest in shallow coastal areas. A single continent has a much smaller shoreline than multiple continents of the same size. Perhaps this restriction of marine habitats contributed to the drastic loss of species, for up to 95% of marine species perished, compared to "only" 70% of land species. Another factor might have been massive basalt flow attributed to the time, which could have increased CO_2 levels to precipitate global warming. Some scientists invoke extraterrestrial causes: a huge meteorite crater discovered in 2006 in Antarctica and dated to between 100 and 500 million years ago could represent an impact which darkened skies, decreased sunlight, and shut down photosynthesis. Although the cause remains unknown, fossils clearly document the fact of Earth's most devastating extinction. The event closed the Paleozoic Era, and inevitably opened the door to a new burst of life in the Mesozoic.

Mesozoic Era: Age of the Dinosaurs

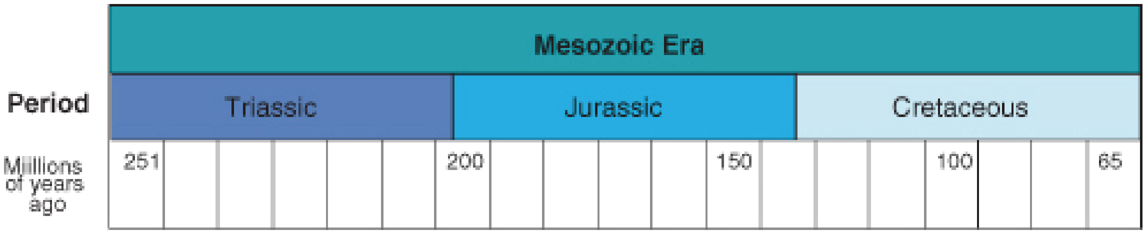

Figure 11.38: (37)

Following the "great dying" at the end of the Permian, a resurgence of evolution in the Mesozoic established the basis of modern life (**Figure** 11.38). The continents, which began as one, broke apart and eventually shifted into their present configuration. Rifting encouraged speciation (**Figure** 11.39). Relatively stable warm temperatures contributed once again to great diversification among animals.

During the **Triassic**, early dinosaurs appeared on land as the archosaurs, in the ocean as ichthyosaurs, and in the air as pterosaurs (**Figure** 11.40). One line of reptiles gave rise to the first mammals and others to the earliest turtles and crocodiles. Seed ferns and conifers dominated the forests. Modern corals and fishes, and many modern insects, evolved. The Triassic gave way to the Jurassic with one of the most active periods of volcanism ever recorded. Pangaea began to break apart. The major extinction marking the border between these two Periods opened niches which made way for the Age of the Dinosaurs.

The **Jurassic Period** was the golden age of the large dinosaurs which lived amidst warm, fern-and cycad-filled forests of pines, cedars, and yews (**Figure** 11.41). Dinosaurs included widespread and huge herbivorous sauropods, smaller predatory theropods, stegosaurs, and

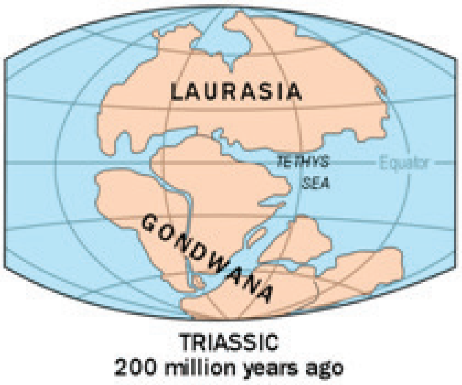

Figure 11.39: A major geological change in the Mesozoic was the breakup of the supercontinent Pangaea into Laurasia and Gondwana, and eventually into the continents we know today. The breakup created new niches, contributing to speciation. (12)

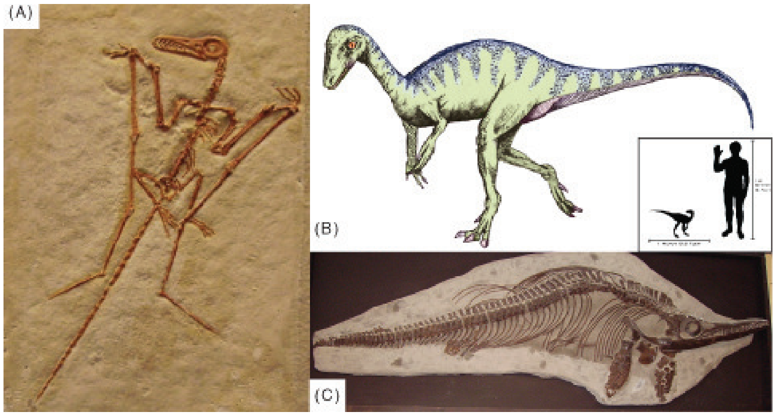

Figure 11.40: Early dinosaurs branched off from other reptiles in the Triassic. The dinosaurs radiated into diverse niches – many undoubtedly newly opened by the massive Permian extinction. Pterosaurs (A) inhabited the air, archosaurs (B) the land, and ichthyosaurs (C) the seas. Not all dinosaurs were giant, as the size comparison of archosaurs to the average adult human (B, inset) shows. (33)

pterosaurs. Ichthyosaurs and plesiosaurs thrived in the oceans. Ammonites, sea urchins, and starfish were abundant invertebrates. The first birds and lizards appeared. One of the most famous transition fossils, **Archaeopteryx**, with characteristics of both reptiles and birds, dates from this Period (**Figure** 11.42). During the Jurassic, the supercontinent Pangaea broke apart into Laurasia and Gondwana.

Figure 11.41: The Jurassic was the golden age of large dinosaurs. Coniferous trees, also huge, and fern and cycad swamps formed their habitats. (41)

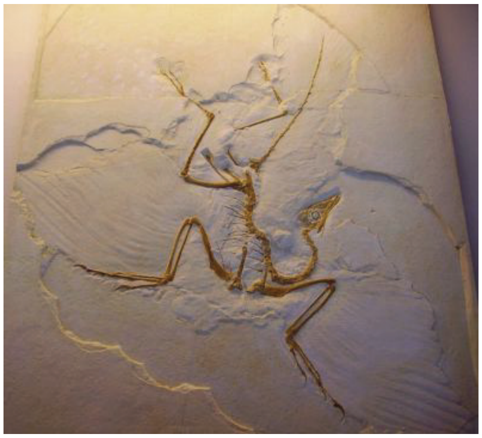

Figure 11.42: One of the most famous of all transitional fossils is *Archaeopteryx,* “ancient wings.” The fossil dates back to the Jurassic. Both reptilian features (teeth and claws) and avian features (wings and feathers) are clear. (34)

Flowering plants first appeared in the Jurassic, but dominated the last, **Cretaceous Period** of the Mesozoic.

- New kinds of insects coevolved with the flowering plants, serving as their pollinators.

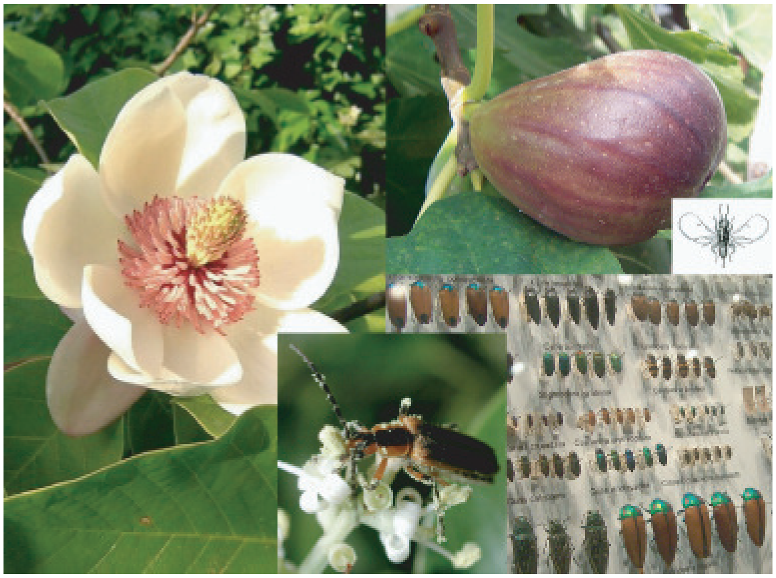

Figure 11.43: Plants first evolved flowers during the Cretaceous. Flowers attracted and fed insects, and insects, in turn, pollinated the flowers, leading to a long coevolutionary relationship. Cretaceous examples include the magnolia and its beetle pollinators (left and below), and the unique fig "fruit"-flower and its tiny wasp pollinator (top right). (35)

An early example of this coevolution is the magnolia, which developed flowers to attract – and withstand feeding damage from - beetle pollinators. Bees first appeared during the Cretaceous, and figs evolved unusual flower-fruits in concert with tiny wasp pollinators (**Figure** 11.43).

- Primitive birds arose from reptilian ancestors and soon out-competed many of the pterosaurs.
- All three major groups of mammals – **monotremes**, **marsupials**, and **placentals** – became established, but remained small.

In part because a huge sea (the Tethys) formed an east-west connection between the oceans, Cretaceous climate was uniformly warm; even the poles lacked ice. In response, warm-adapted plants and dinosaurs expanded to within 15 degrees of the poles. Dinosaurs reached a peak of diversity and size (**Figure** 11.44 and **Figure** 11.45).

- Titanosaurs, including possibly the largest of all the dinosaurs, the 100-ton *Argentinosaurus*, were the dominant herbivores. A single *Argentinosaurus* vertebra was 1.3 meters long, and its tibia would have been as tall as some humans. Fossilized eggs, containing embryos with skin, indicate that titanosaurs were colonial nesters. Fossilized

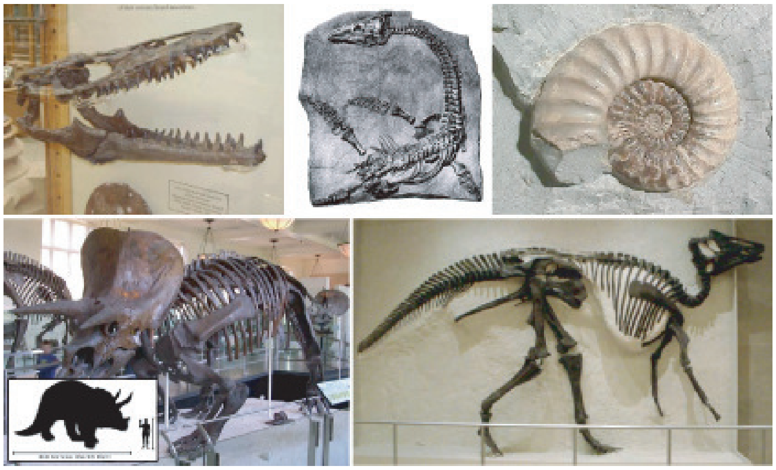

Figure 11.44: Many kinds of reptiles and invertebrates lived during the Cretaceous Period. Mosasaurs (upper left), plesiosaurs (center) and ammonites (upper right) swam the seas with modern sharks. Triceratops (lower left) and duckbilled dinosaurs (lower right) show some of Cretaceous diversity in dinosaurs. (42)

Figure 11.45: Moderate climate worldwide during the Cretaceous encouraged great size and diversification among dinosaurs. The herbivorous titanosaur, *Argentinosaurus* (above) may have been the largest of all the dinosaurs, weighing in at up to 100 tons. *Gigantosaurus* (below) probably preyed upon titanosaurs such as *Argentinosaurus*, but weighed "only" 5.2 tons, and despite a bath-tub-sized skull, operated on a brain the size of a banana. (27)

dung shows they ate cycads and conifers, but also palms and the ancestors of rice and bamboo; some scientists suggest that dinosaurs and grasses coevolved like insects and flowering plants.
- One of the largest predatory dinosaurs,*Giganotosaurus*, weighed "only" 5.2 tons, but in length surpassed *Tyrannosaurus* rex by two meters (six feet). *Giganotosaurus'* skull was the size of a bathtub, but its brain was the size and shape of a banana! What were they *thinking*?

The dramatic extinction of all dinosaurs (except the lineage which led to birds) marked the end of the Cretaceous. Dinosaurs had begun to decline earlier, perhaps due to reduction in atmospheric oxygen and global cooling. A worldwide iridium-rich layer, dated at 65.5 million years ago, provides evidence for an additional, more dramatic cause for their ultimate extinction. Iridium is rare in the Earth's crust, but common in comets and asteroids. Scientists correlate this layer with a huge crater in the Yucatan and Gulf of Mexico. A collision/explosion between the Earth and a comet or asteroid could have spread debris which set off tsunamis, altered the climate (including acid rain), and reduced sunlight 10-20%. A consequent reduction in photosynthesis would have caused a drastic disruption in food chains. Some scientists believe that volcanism also contributed to the **"K-T"** (Cretaceous-Tertiary) **extinction**, but most agree that "an impact event" was at least a major cause (**Figure** 11.46). The massive extinction and sharp geologic line led geologists to define the end of the Mesozoic and the beginning of our modern Era, the Cenozoic, with this event.

Figure 11.46: The extinction of the dinosaurs at the end of the Cretaceous is attributed at least in part to an impact event which could have involved a meteor, an asteroid, or a comet. (21)

Cenozoic Era: Age of Modern Life

Neogene and Quaternary (Q) Periods share part of the Pliocene Epoch (Pl). Pleistocene (P) and Holocene (H) Epochs complete the Quaternary Period. Divisions in this part of the

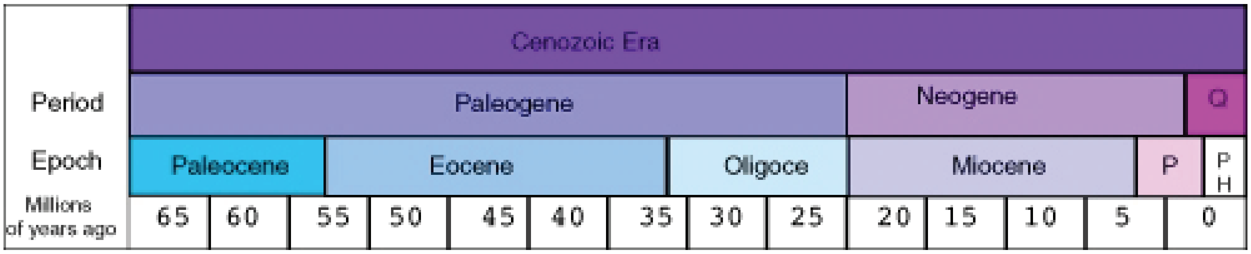

Figure 11.47: (23)

Time Scale are debated and may change.

The **Cenozoic Era** brings the history of life into the present, but not without drama, mystery, and the looming possibility of a "Sixth Extinction" (**Figure** 11.47) You probably know the basic story: mammals took over where dinosaurs left off, branched to form primates, moved to the grasslands, became human-like, survived the ice ages, and the rest is – literally – history. Let's look at some of the major events, focusing not only on our immediate ancestors but also on the world in which they evolved. More detailed stories of the evolution of humans and other groups will be told in later chapters.

Seven Epochs comprise the Cenozoic Era, with the Holocene continuing up to today. "Tertiary" refers to the 64 million years and five epochs before the Quaternary Period, well known for its recent ice ages and recognizable humans. Tertiary and Quaternary periods could be called suberas, but current organization of the Cenozoic segment of the Geologic Time Scale is the subject of current debate; it may well change.

The **Paleocene Epoch** provided a worldwide warm, humid climate for the rapid evolution which followed the extinction of the dinosaurs (**Figure** 11.48). Many plants, herbivores, and carnivores had disappeared because they depended on photosynthesis, but omnivores, insectivores, and scavengers – which included many mammals and birds – survived because their food sources actually increased. Mammals radiated into the ecological niches opened up by the extinction of herbivores and carnivores, and larger species, up to bear- or hippopotamus-sized, began to appear In equatorial regions, the first recognizably modern rain forests appeared, and south of the equator, hot arid regions provided niches for new groups of plants, including cacti.

Volcanism or a massive release of methane gas trapped in the oceans may have triggered one of the most rapid global warming events ever measured at the beginning of the **Eocene**, 56 million years ago. CO_2 from either volcanism or oxidation of methane would have caused the oceans to become more acidic, and Earth's temperatures to rise. Warm temperatures allowed forests of dawn redwood, swamp cypress, and palms to extend toward both poles. In the interiors of the continents, seasonal temperature and moisture variations led to the evolution of grasses, expansive savannas and deciduous forests. Within these new ecosystems, modern mammals with specialized teeth evolved. Probably due to high temperatures, these mammals were smaller than those who preceded them – or those who followed:

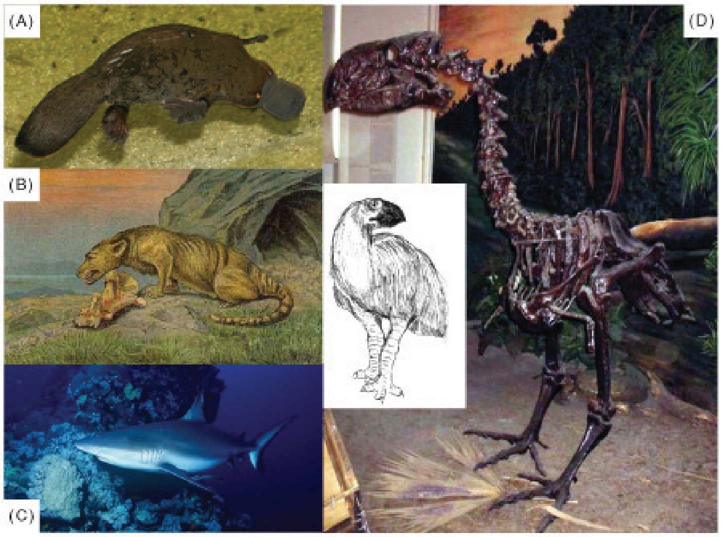

Figure 11.48: During the Paleocene, mammals and birds invaded ecological niches formerly occupied by the dinosaurs. Mammals included monotremes (A), marsupials, and hoofed placentals (B). Modern sharks (C) patrolled the seas. Birds included the giant flightless *Gastornis* (D). (53)

- Horses and tapirs evolved in North America, and rhinoceros evolved in Asia.
- Primates, with their long arms and legs and grasping hands and feet, appeared.
- Mammals returned to the sea; *Basilosaurus* was an ancestor of today's whales.

At the beginning of the Eocene, Australia was still connected to Antarctica, but when they broke apart, ocean currents changed and cooling began in earnest, foreshadowing the ice ages to come. Tundra ecosystems developed near the poles. Falling sea levels, a land bridge immigration of mammals from Asia to North America, and perhaps several impact events led to an extinction which marks the end of this epoch.

As its name implies, the Oligocene Epoch produced a "few" new mammals, especially in grasslands and savannahs (**Figure** 11.49).

- Pig-like entelodonts used massive skulls to crush bones of scavenged prey.
- One of the largest land mammals of all time, the 18-foot, 15 ton *Indricotherium*, ate leaves from the tops of trees in the manner of a giraffe.
- Horses, represented by *Mesohippus* remained small relative to today's species.
- Large terrestrial carnivores such as *Hyaenodon*, hunted mammals up to the size of sheep.
- The rhinoceros-like *Arsinoitherium* wandered tropical rain forests and swamps.

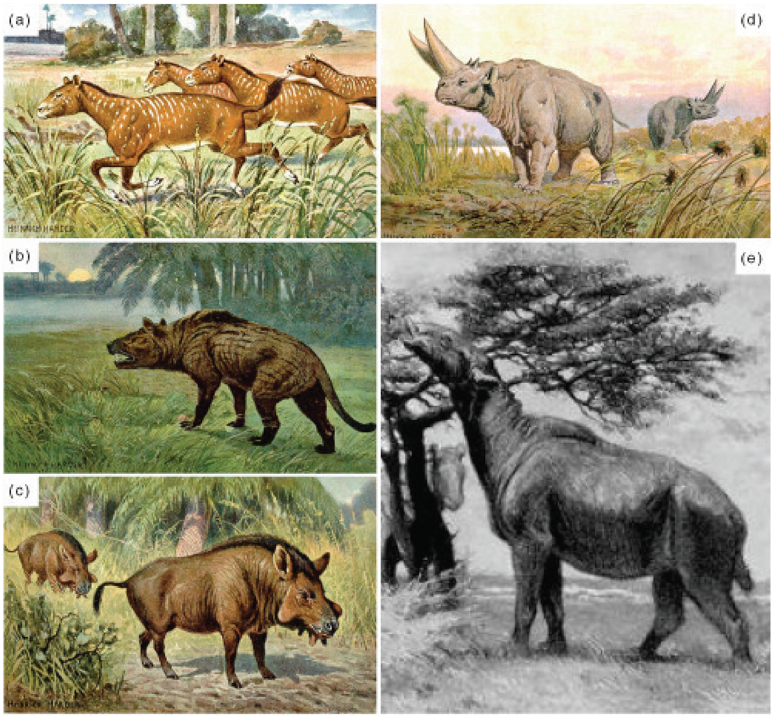

Figure 11.49: The Oligocene produced fewer new mammals than the Eocene; most were adapted to grasslands. *Mesohippus* (A) showed small steps toward modern horses. *Hyaenodon* (B) had the large, sharp teeth of a carnivore. *Elotherium* (C) was a piglike scavenger, and *Arsinoitherium* (D) was a large relative of elephants and hyraxes. Perhaps the largest land mammal of all time resembled an overweight giraffe; *Indricotherium* (E) weighed up to 15 tons and reached 18 feet in height. (31)

By the beginning of the **Miocene Epoch** 23 million years ago, the continents had almost assumed their current configuration, except that North and South America did not connect. Oceans continued to cool, ice caps expanded at the poles, and consequently the climate dried. Grasslands, needing less rain, replaced forests, and large herbivores coevolved with the grasses. Modern mammals, including wolves, beaver, deer, camels, seals, dolphins, and porpoises, evolved. Up to 100 species of apes lived throughout Africa, Europe, and Asia. Almost all modern bird groups were represented.

The Earth's climate continued to cool into the **Pliocene**, the epoch in which hominids first appeared. Seasons became more pronounced; deciduous forests and grasslands replaced tropical forests, and coniferous forests and tundra expanded. Large mammals, such as browsing mastodons and grazing mammoths, roamed the grasslands and tundra. Into this setting walked Australopithecines, such as **Lucy** who share common ancestry with humans. Fossil footprints dated as 3.7 million years old establish Australopithecenes as bipedal – perhaps the first apes to walk upright (**Figure** 11.50). Later Pliocene hominids included two members of our own genus, *Homo rudolfensis* and *Homo habilis*. During this epoch, falling sea levels exposed two land bridges which allowed important migrations.

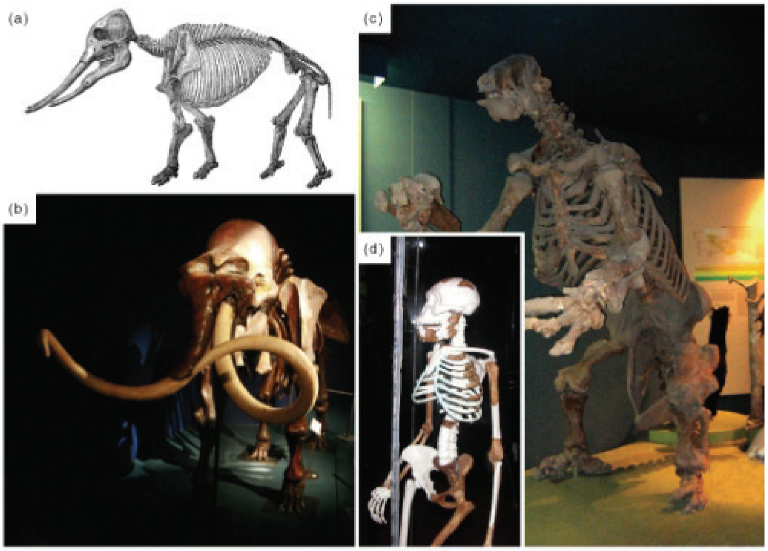

Figure 11.50: Lucy (D) is one of the most complete fossils of *Australopithecus afarensis*, a human relative also known for fossil footprints which establish an upright posture. Note that the brown bones are Lucy's; others have been added to restore her skeleton. Australopithecines coexisted (but not necessarily on the same continent!) with browsing mastodons (A), grazing mammoths (B), and giant herbivorous sloths (C). (14)

- One allowed horses, mammoths, mastodons and more to migrate between Asia and North America.

- A second allowed North American placental mammals, such as giant sloths, armadillos, and sabertooth cats, to migrate to South America. Placentals eventually out-competed all of South America's marsupials except the opossum.

Repeated glaciations define the **Pleistocene Epoch**. Glaciation tied up huge volumes of water in ice packs; rainfall was less, because evaporation was less. Deserts were relatively dry. During interglacial periods, huge inland lakes and rivers held or carried the melt waters, and coastal flooding reduced land area. During the four major glaciations, these severe climate changes stressed animals and plants, encouraged the evolution of large animals (the **Pleistocene megafauna**), and forced life toward the equator.

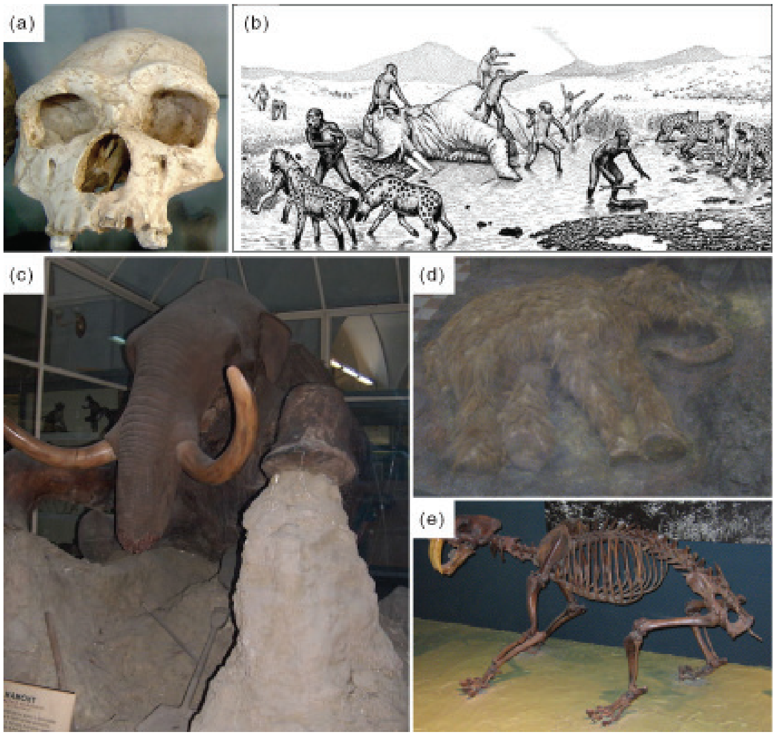

Figure 11.51: That *Homo erectus* (A), and later (or in other parts of the world) *Homo habilis*, hunted mammoth (B) is shown by fossil evidence 1.8 million years old. Woolly mammoths (C), specially adapted to cold climate, were probably hunted, as well, as humans spread throughout the world. Nearly 40 woolly mammoth remains have been found preserved in permafrost, complete with soft tissue and DNA. To date, mitochondrial DNA has been sequenced. The calf (D) measures 2.3 meters (8 feet) long. A predatory competitor to humans was the saber-tooth tiger, (E). (52)

- Some adapted to the cold: the Woolly Mammoth grew thick, shaggy hair oiled by abundant sebaceous glands, a layer of fat beneath the skin, smaller ears, and even a convenient flap to cover the anus, keeping out the cold. Mammoth teeth ground tough tundra grasses, and their long, curved tusks may have helped to clear snow. Permafrosts have preserved nearly 40 mammoth remains, including soft tissues, and scientists actually hope to be able to recreate its genome; mitochondrial DNA for one species has already been sequenced! Using this sequence as a molecular clock, scientists calculate that mammoths diverged from African elephants about 6 million years ago, roughly the same time that humans diverged from chimpanzees.

- Saber-tooth cats used dagger-like teeth to cut their prey's windpipe and jugular veins, causing death by bleeding. Many saber-tooths have been found in the LaBrea Tar Pits in southern California, where they had tried to feed on mammoths trapped before them in the sticky tar/asphalt.
- *Homo erectus,* the dominant hominid during the Pleistocene, migrated throughout Africa, Europe, and Asia, giving rise to a number of variations of hominids. Although *Homo erectus* was probably the first hominid to leave Africa, the species may not have been a direct ancestor of humans. Pleistocene hominids were hunter-gatherers; evidence dated at 1.8 million years ago supports their consumption of mammoth.

A major extinction of Pleistocene megafauna continued into the Holocene. Some attribute the extinction to changing climate or disease, but others have connected the migrations of humans to each continent's time of extinction The "overkill" theory suggests that humans hunted large animals with too much success. Agreement is not yet universal, but most scientists admit the evidence is strong.

The current **Holocene Epoch** began 11,550 years ago (about 9600 B.C.) with the retreat of the Pleistocene glaciers. During the Holocene, melting ice has raised sea level over 180 meters (600 feet). Geologists believe that we are currently experiencing an interglacial warming, and that glaciers will return – unless continued human burning of fossil fuels raises CO_2 levels to bring about global warming. All of human civilization has occurred within the Holocene; *Homo sapiens* have passed through Mesolithic, Neolithic, and Bronze Age civilizations. Human evolution will be discussed in more detail in a future chapter, but here we will examine the possibility that humans are currently causing a mass extinction which some compare to the Permian. Many would include the Pleistocene megafauna in this "Sixth Extinction," citing the "overkill theory" data in **Figure** 11.52. Some even call the period of time from that loss to the present the "Anthropocene epoch" to describe the major impact humans have had on the planet and its life. Human population has surpassed 6.6 billion, and over-fishing, climate change, industrialization, intensive agriculture, and clearance of grasslands and rainforests contribute to a startlingly high loss of life.

Paleontologists estimate that background extinction rates throughout most of life's history averaged between 1 and 10 species per year (**Figure** 11.53) . The present rate of extinction is thought to be 100 to 1000 times "background" rates, suggesting that the number of species which currently disappear *each year* could exceed 1,000! Biologist E.O. Wilson has predicted that current rates will result in the loss of over half of life's biodiversity within the next one hundred years. In contrast, Earth's shortest previous extinctions spanned several hundred thousand to several million years, and evidence for cause is entirely geological in nature. No

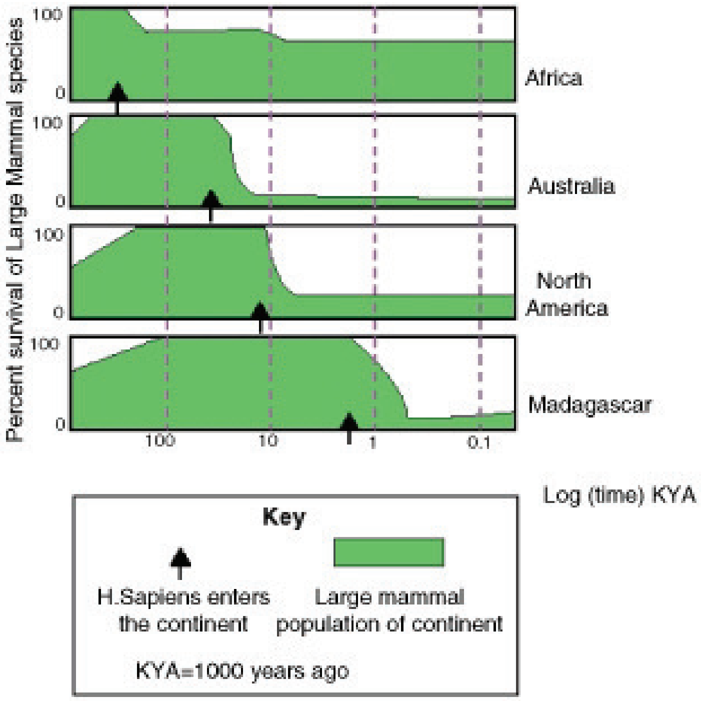

Figure 11.52: This data comparing the arrival of humans to the decline of the Pleistocene megafauna supports the "overkill" theory that human predation contributed to the extinction of large mammals throughout the world. Other theories involve climate change and disease. (3)

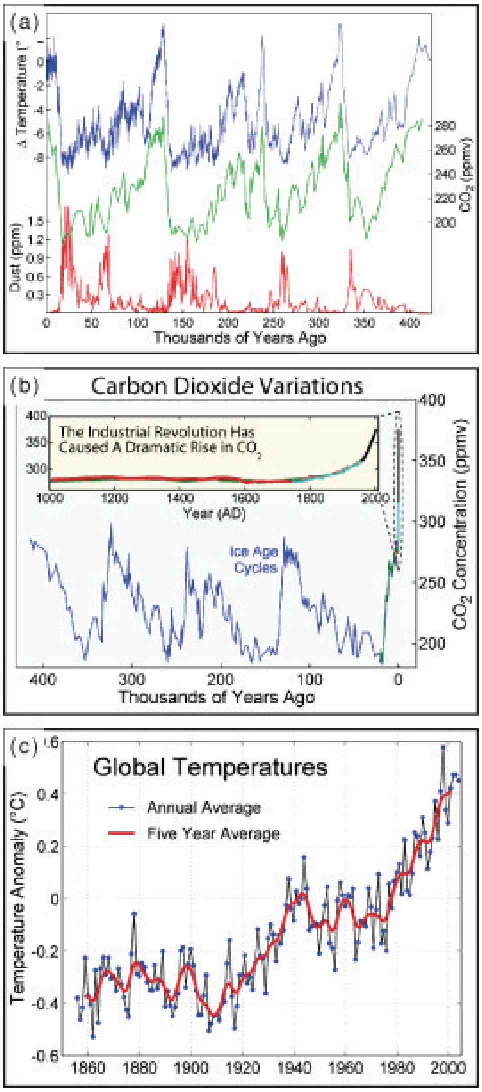

Figure 11.53: (A) Changes in CO_2 levels (green) are clearly associated with temperature changes (blue); the graph shows the four major Ice ages of the Pleistocene. Graphs B (long time scale) and C (recent time) show increases in CO_2 and global temperature over the past 150 years, suggesting that the Industrial Revolution, which began our major fossil fuel burning and release of CO_2, may account for much of the increase in temperature – a new, human–induced global warming. (4)

other species has influenced the Earth and its life as powerfully as *Homo sapiens.*

Others say there is ample evidence – evidence discussed in this lesson – to show that extinction is a natural phenomenon which has occurred repeatedly throughout the history of life on Earth. They point to the recoveries – indeed, radiations – which filled vacated ecological niches after each event.

However, those who are concerned about the current extinction wonder whether or not humans will be one of the species to become extinct. Because we are the only surviving members of our family, recovery or radiation would not be an option.

What do you think?

Lesson Summary

- After 3 billion years, life was unicellular but included all 3 major lineages: Bacteria, Archaea and Eukaryotes; all of multicellular evolution occurred within the last billion years.
- Plant, animal, and fungal ancestors diverged as solitary cells.
- Colonies of eukaryotic cells and specialized cells evolved; *Volvox* illustrates this level of evolution.
- Sexual reproduction appeared a little over 1 billion years ago, providing more variation for natural selection.
- By about 1 billion years ago, true (multicellular) plants emerged, and 100 million years later, true animals.
- 600 million year old Ediacaran fossils illustrate diverse early animal life, but few are related to modern animals.
- The Cambrian explosion was the sudden appearance of great diversity in animals, plants, and fungi clearly related to modern species, due to lower O_2, global warming, plate tectonics, and a critical mass of biotic change.
- During the Ordovician, liverworts became the first land plants, and jawless, bony-plated fish joined a variety of invertebrates in warm seas.
- Ferns and the first seed plants forested the land in the Devonian; in shallow seas, jawed fish evolved lobed fins.
- Extensive coal deposits and an all-time high level of atmospheric O_2 characterized the Carboniferous Period. Giant insects, early gymnosperms with pollen, and vertebrates with shelled eggs colonized dry land.
- During the Permian, all the major landmasses of earth combined into a single supercontinent, Pangaea. A continental climate of seasons and drought favored reptiles, gymnosperms, and insects such as beetles. The Permian ended with the most massive extinction of all time; 99.5% of all species disappeared, opening the door for a new radiation of species in the Mesozoic.
- The Permian extinction, stable temperatures and continental breakup created niches

for a great radiation of life in the Triassic Period. Reptiles diversified – on land as the archosaurs, in the air as pterosaurs, and in the seas as ichthyosaurs. Other reptilian lines gave rise to early turtles, crocodiles, and finally, mammals and birds.
- During the Cretaceous, primitive birds began to radiate and out-compete the pterosaurs; dinosaurs reached their largest size and greatest diversity.
- Record-high temperatures during the Eocene made way for hoofed animals and primates within grasslands, savannas, and deciduous and coniferous forests.
- *Australopithecus*, perhaps the earliest, upright hominid, appeared during the Pliocene. Global cooling and glaciation led to a drop in sea level, exposing two land bridges which allowed important animal migrations.
- Cycles of glaciation stressed Pleistocene animals and plants; some, like the woolly mammoth, adapted to cold and others, like *Homo erectus*, the dominant hominid, migrated throughout Africa, Europe, and Asia.
- As the human population climbs above 6.6 billion, we may be causing a Sixth Extinction of life on Earth.

Review Questions

1. What major evolutionary steps followed the evolution of the first eukaryotic cell during the late Precambrian to set the stage for the "Cambrian explosion?"
2. List the global environmental factors which influenced the evolution of multicellular life.
3. Discuss and give examples of the relationships among the environmental factors you listed above. Include their major effects on the history of life.
4. Describe the conditions under which the dinosaurs emerged to dominate life on Earth, and identify the diversity of habitats and niches occupied by the dinosaurs during their "golden age."
5. What famous example of coevolution began in earnest during the Cretaceous? Give two early examples.
6. Cite and evaluate the evidence for an "impact event" as the primary cause of the K-T extinction.
7. Analyze the emergence of mammals and birds as dominant land animals during the early Cenozoic.
8. How does the Cenozoic climate explain the emergence of grassland and tundra and their megafauna?
9. Give two examples of how land bridge formation can affect evolution.
10. Discuss the factors which are contributing to the current major extinction, and analyze your own response to E.O. Wilson's description of the "Sixth Extinction."

Further Reading / Supplemental Links

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Vocabulary

Archaeopteryx One of the most famous transition fossils; has characteristics of both reptiles and birds.

Cambrian explosion The abrupt emergence of many new species during the Cambrian Period.

liverworts Among the first true plants; colonized land during the Ordovician.

Jurassic Period The golden age of the large dinosaurs which lived amidst warm, fern-and cycad-filled forests of pines, cedars, and yews.

Lucy One of the most complete fossils of *Australopithecus afarensis*, a human relative also known for fossil footprints which establish an upright posture.

marsupials One of the three major groups of mammals.

monotremes One of the three major groups of mammals.

Pangaea A single supercontinent formed from all the major land masses of Earth; formed during the Permian.

placentals One of the three major groups of mammals.

trilobites Common arthropods which were diverse and abundant during the Cambrian Period.

Points to Consider

- The study of the history of life attempts to answer the age-old question: where did we humans come from? What are some of the answers our current knowledge gives us? What points are still missing?
- To what extent has life itself influenced the history of life on Earth? Consider some specific effects certain kinds of life have had on climate, the atmosphere, and certain species.
- At least some mammoth DNA has been preserved in permafrost. What do you think about the idea of re-creating animals such as the mammoth from the past – as fictionalized in Jurassic Park?
- Do you think extinction plays an essential role in evolution? Is it a negative or positive role?
- Do you judge the Sixth Extinction to be an important problem? Do you think it is significantly different from earlier extinctions?

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