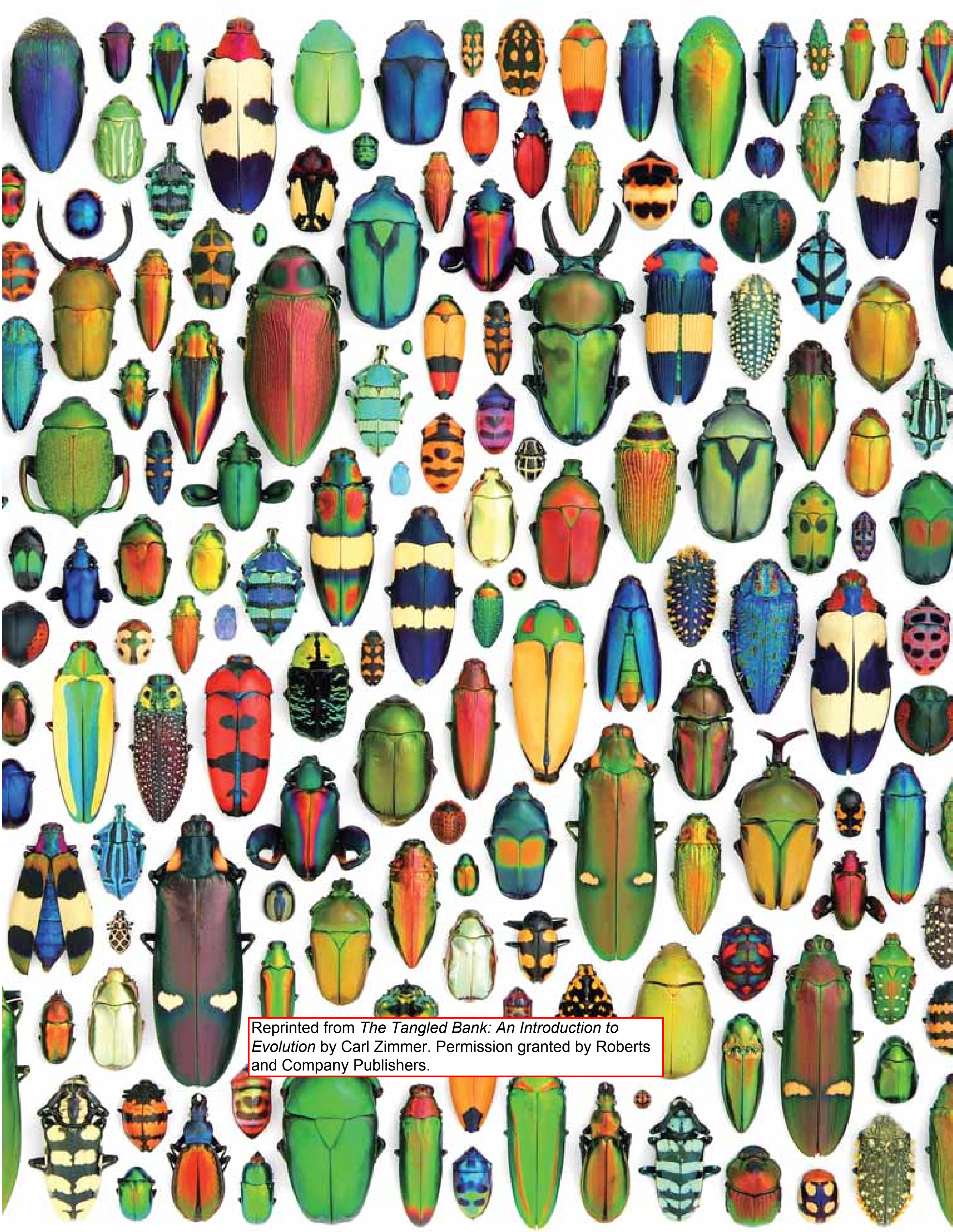


10

Radiations & Extinctions

Biodiversity Through the Ages

There's a story that scientists like to tell about the great evolutionary biologist J. B. S. Haldane. Supposedly, Haldane once found himself in the company of a group of theologians. They asked him what one could conclude about the nature of the Creator from a study of his creation. "An inordinate fondness for beetles," Haldane replied.

There are some 350,000 named species of beetles—70 times more species than all the mammal species on Earth. Insects, the lineage to which beetles belong, include a million named species, the majority of all 1.8 million species scientists have ever described.

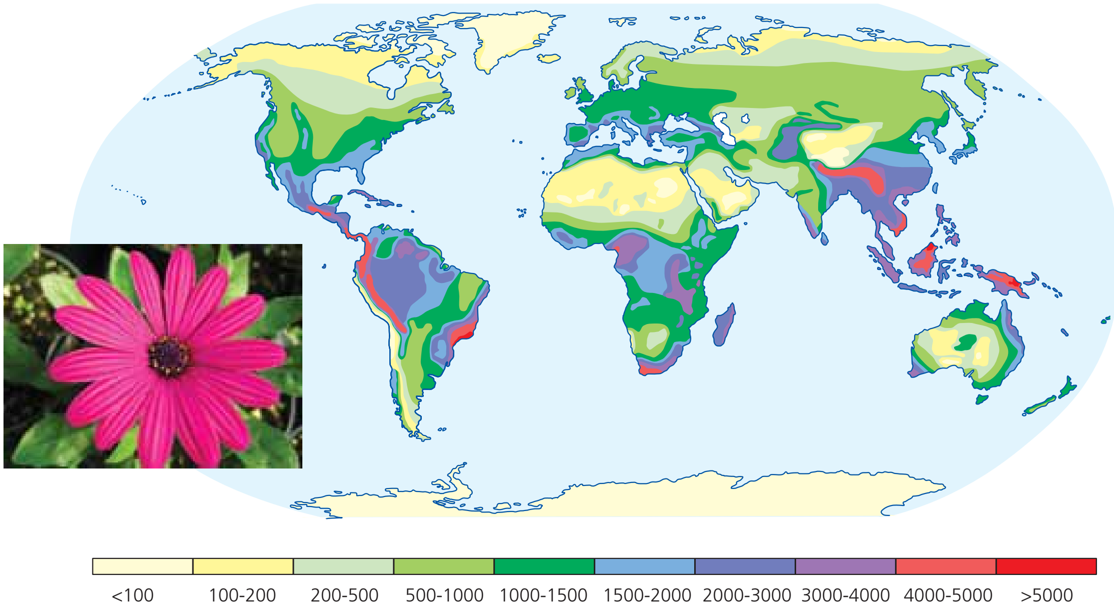


Figure 10.1 The diversity of plants is much higher in the tropics than in the regions near the poles. Animals and other groups of species show a similar pattern of diversity. (Adapted from Benton, 2008)

Biological diversity (or biodiversity for short) is one of the most intriguing features of life. Why are there so many insects on Earth and so few mammals? Why is biodiversity richest in the tropics, rather than being spread smoothly across the planet (**Figure 10.1**)? Why do different continents have different patterns of diversity? Almost everywhere on Earth, for example, placental mammals make up the vast diversity of mammal diversity. On Australia, however, there is a huge diversity of marsupial mammals.

Biodiversity has also formed striking patterns through the history of life, as illustrated in **Figure 10.2**. A large team of scientists produced this graph by analyzing records for 3.5 million fossils of marine invertebrates that lived during the past 540 million years. They divided up that time into 48 intervals and calculated how many genera were alive in each one. The graph shows that among marine invertebrates, biodiversity is higher today than it was 540 million years ago. But the pace of this rise was not steady. There were periods in which diversity rose rapidly, as well as periods in which it dropped drastically.

In this chapter we'll examine how scientists study biodiversity, analyzing patterns over space and time and then creating hypotheses they can test. We'll explore how lineages of species grow, and then how they become extinct. We may, biologists fear, be in the early stages of a catastrophic bout of extinctions on a scale not seen for millions of years. By understanding the past of biodiversity, scientists can make some predictions about the future we are creating.

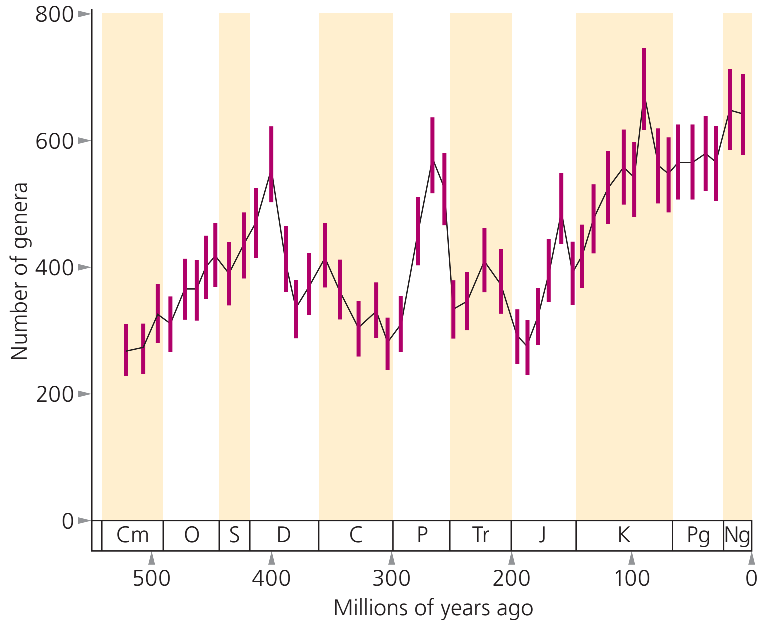


Figure 10.2 A team of paleontologists analyzed 3.5 million fossils of marine invertebrates that lived over the past 540 million years to determine the history of diversity. As this graph shows, diversity has risen and fallen several times, but today there are about twice as many genera as there were at the beginning of this period. (Adapted from Alroy et al., 2008)

Riding the Continents

Few people have heard of the mite harvestman, and fewer still would recognize it at close range. It is related to the far more familiar daddy longlegs, but its legs are stubby rather than long, and its body is about as big as a sesame seed. On the floors of the humid forests where it dwells, it looks like a speck of dirt. As unglamorous as the mite harvestman may seem, however, it has a spectacular history to unfold.

An individual mite harvestman may spend its entire life in a few square meters of forest floor. The range of an entire species may be less than 100 kilometers (60 miles) across. Yet there are 5,000 species of mite harvestman, and they can be found on five continents and a number of islands. Sarah Boyer, a biologist at Macalester College in Minnesota, and her colleagues have traveled around the world to catch mite harvestmen, and they've used the DNA of the animals to draw an evolutionary tree. At first glance, their results seem bizarre. One lineage, for example, is only found in Chile, South Africa, and Sri Lanka—countries separated by thousands of kilometers of ocean (**Figure 10.3**).

But the results of Boyer's research make sense if you remember that Chile, South Africa, and Sri Lanka have not always been where they are today. Over millions of years, continents have slowly moved across the globe. Mite harvestmen belong to an ancient lineage; fossils show that they branched off from other invertebrates at least 400 million years ago. Back then, much of the world's land

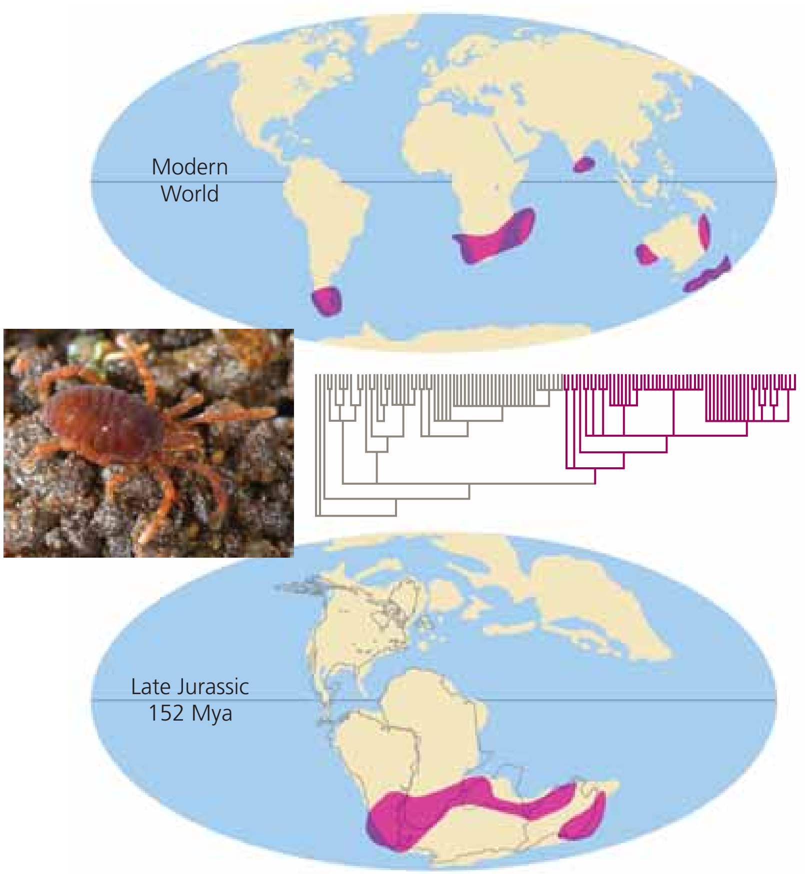


Figure 10.3 One lineage of mite harvestmen can be found on continents and islands separated by thousands of miles of ocean. They reached their present locations thanks to continental drift. Around 150 million years ago, the ranges of these invertebrates formed a continuous belt. Later, the continents broke apart and moved away, taking the mite harvestmen with them. (Adapted from Boyer et al., 2007)

was fused together in a single supercontinent. When Boyer mapped the locations of the mite harvestmen on a map of ancient Earth, she found that they were all close to each other in the Southern Hemisphere.

The study of how biodiversity is spread around the world is known as biogeography. Mite harvestmen illustrate one of the most common patterns in biogeography, called vicariance: species become separated from each other when geographical barriers emerge. Those barriers can be formed by oceans, as in the case of the mite harvestmen; they can also be separated by rising mountains, spreading deserts, and shifting rivers. The other major pattern in biogeography, known as dispersal, occurs when species themselves spread away from their place of origin. Birds can fly from one island to another, for example, and insects can float on driftwood.

The biogeography of many groups of species is the result of both dispersal and vicariance. Most living species of marsupials can be found today on Australia and its surrounding islands. But marsupials originally evolved thousands of kilometers away (**Figure 10.4**). The oldest fossils of marsupial-like mammals, dating back 150 million years, come from China. At the time, Asia was linked to North America, and by 120 million years ago marsupials had spread there as well. Many new lineages of marsupials evolved in North America over the next 55 million years. From there, some of these marsupials spread to Europe, even

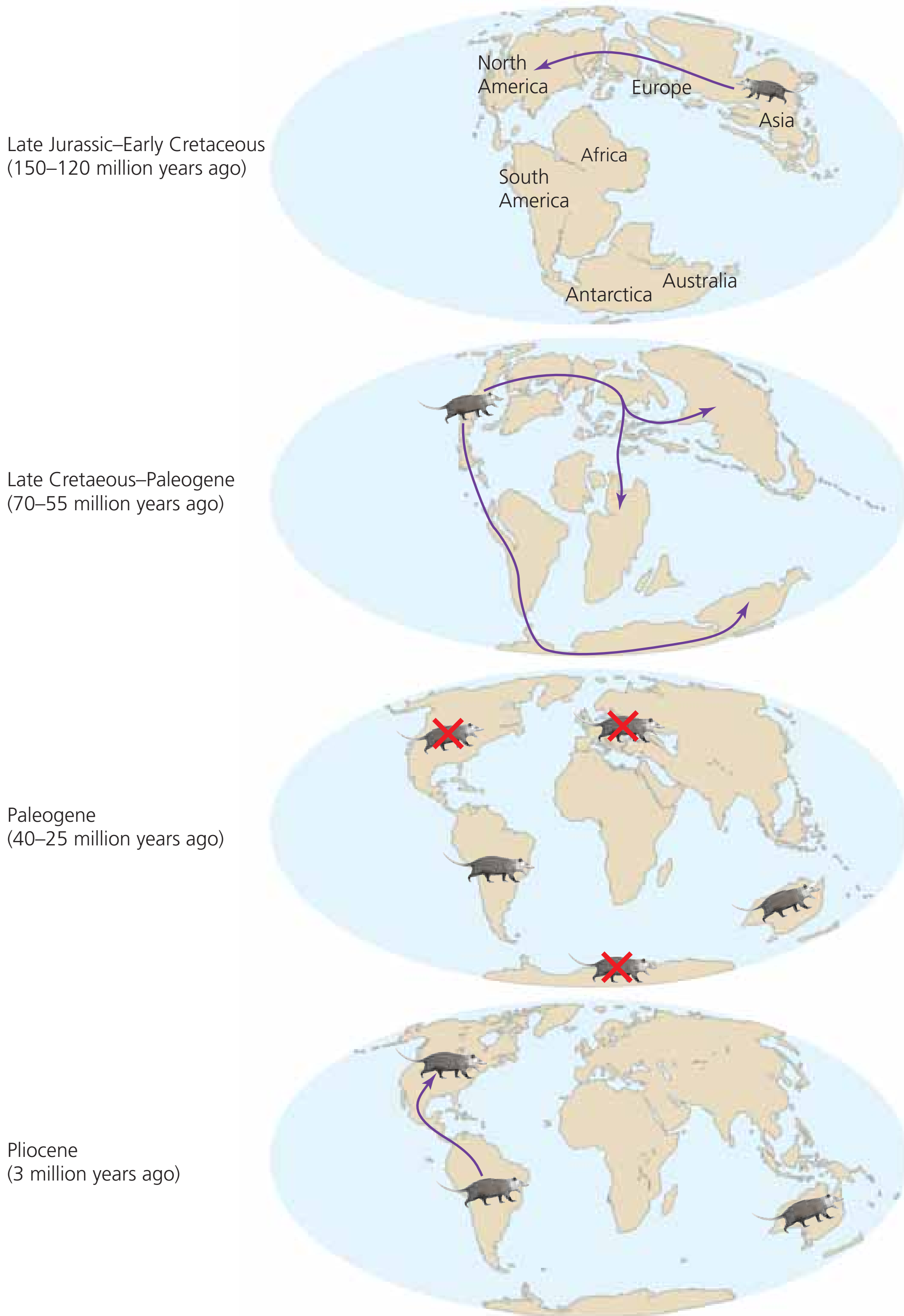


Figure 10.4 The fossil record sheds light on the spread of marsupial mammals around the world.

reaching as far as North Africa and Central Asia. All of these northern hemisphere marsupials eventually died out in a series of extinctions between 30 and 25 million years ago.

But marsupials did not die out entirely. Another group of North American marsupials dispersed to South America around 70 million years ago. From there, they expanded into Antarctica and Australia, both of which were attached to South America at the time. Marsupials arrived in Australia no later than 55 million years ago, the age of the oldest marsupial fossils found there. Later, South America, Antarctica, and Australia began to drift apart, each carrying with it a population of marsupials. The fossil record shows that marsupials were still in Antarctica 40 million years ago. But as the continent moved nearer to the South Pole and became cold, these animals became extinct.

In South America, marsupials diversified into a wide range of different forms, including cat-like marsupial sabertooths. These large carnivorous species became extinct, along with many other unique South American marsupials, when the continent reconnected to North America a few million years ago. However, there are still many different species of small and medium-sized marsupials living in South America today. One South American marsupial, the familiar Virginia opossum, even recolonized North America.

Australia, meanwhile, drifted in isolation for over 40 million years. The fossil record of Australia is too patchy for paleontologists to say whether there were any placental mammals in Australia at this time. Abundant Australian fossils date back to about 25 million years ago, at which point all the mammals in Austrlia were marsupials. They evolved into a spectacular range of forms, including kangaroos and koalas. It was not until 15 million years ago that Australia moved close enough to Asia to allow placental mammals—rats and bats—to begin to colonize the continent. These invaders diversified into many ecological niches, but they don't seem to have displaced any of the marsupial species that were already there.

Isolated islands have also allowed dispersing species to evolve into remarkable new forms. The ancestors of Darwin's finches colonized the Galápagos Islands two to three million years ago, after which they evolved into 14 species that live nowhere else on Earth. On some other islands, birds have become flightless. On the island of Mauritius in the Indian Ocean, for example, there once lived a big flightless bird called the dodo. It became extinct in the 1600s, but Beth Shapiro, a biologist now at the Pennsylvania State University, was able to extract some DNA from a dodo bone in a museum collection. Its DNA revealed that the dodo had a close kinship with species of pigeons native to southeast Asia. Only after the ancestors of the dodos diverged from flying pigeons and ended up on the island of Mauritius did they lose their wings and become huge land-dwellers. A similar transformation took place on Hawaii, where geese from Canada settled and became large and flightless.

Hawaiian geese and dodos may have lost the ability to fly for the same reason. The islands where their flying ancestors arrived lacked large predators that would have menaced them. Instead of investing energy in flight muscles that they never needed to use, the birds that had the greatest reproductive success were the ones that were better at getting energy from the food that was available on their new island homes.

The Pace of Evolution

Biodiversity forms patterns not just across space, but also across time. New species emerge, old ones become extinct; rates of diversification speed up and slow down. These long-term patterns in evolution get their start in the generation-to-generation processes of natural selection, genetic drift, and reproductive isolation.

When a lineage of organisms evolves over a few million years, these processes can potentially produce a wide range of patterns (see **Figure 10.5**). Natural selection may produce a significant change in a trait such as body size, for example. On the other hand, the average size of a species may not change significantly at all (a pattern known as stasis). Stabilizing selection can produce stasis by eliminating the genotypes that give rise to very big or very small sizes. It's also possible for a species to experience a lot of small changes that don't add up to any significant trend. (This type of pattern is known as a random walk, because it resembles the path of someone who randomly chooses where to take each new step.)

At the same time, a species can split in two. The rate at which old species in a lineage produce new ones can be fast or slow (see **Figure 10.5c**). Over millions of years, one lineage may split into a large number of new species, while a related

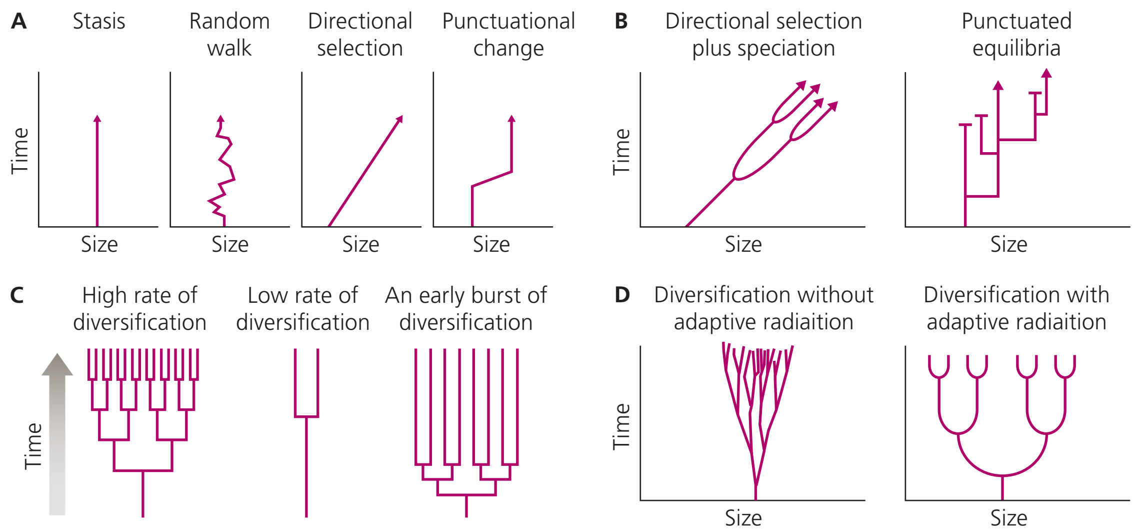


Figure 10.5 Over long periods of time, evolution can form many patterns. A: A trait, such as size, may be constrained by stabilizing selection, undergo small changes that don't add up to a significant shift, experience long-term selection in one direction, or experience a brief punctuation of change. B: A lineage may also branch into new species while experiencing different kinds of morphological change. C: The rate at which new species evolve is different in different lineages. It can also change in a single lineage. D: In an adaptive radiation, a lineage evolves new species and also evolves to occupy a wide range of niches.

lineage hardly speciates at all. It's also possible for a lineage's rate of speciation to slow down or speed up.

Even as new species are evolving, however, others may become extinct. The rate at which species become extinct may be low in one lineage and high in another. It's also possible for the rate of extinction to rise, only to drop again later.

All of these processes can also unfold at the same time, and so the range of possible long-term patterns in evolution can be enormous. A lineage with a low rate of speciation may end up enormously diverse because its rate of extinction is even lower. On the other hand, a lineage that produces new species at a rapid rate may still have relatively few species if those species become extinct quickly. Evolutionary change may happen mainly within the lifetime of species, or it may occur in bursts when new species evolve. A lineage may produce many species that are all very similar to each other, or evolve a wide range of forms.

Any one of these patterns is plausible, given what biologists know about how evolution works. Which of these patterns actually dominate the history of life is a question that they can investigate by studying both living and extinct species.

Evolutionary Fits and Starts

One of the most influential studies of the pace of evolutionary change was published in 1971 by two young paleontologists at the American Museum of Natural History named Niles Eldredge and Stephen Jay Gould. They pointed out that the fossils of a typical species showed few signs of change during its lifetime. New species branching off from old ones had small but distinctive differences. Eldredge carefully documented this stasis in trilobites, an extinct lineage of armored arthropods. He counted the rows of columns in the eyes of each subspecies. He found that they did not change over six million years.

Eldredge and Gould proposed that this pattern was the result of stasis punctuated by relatively fast evolutionary change, a combination they dubbed punctuated equilibria. They argued that natural selection might adapt populations within a species to their local conditions, but overall the species experienced very little change in its lifetime. Most change occurred when a small population became isolated and branched off as a new species. Eldredge and Gould argued that paleontologists could not find fossils from these branchings for two reasons: the populations were small, and they evolved into new species in just thousands of years—a geological blink of an eye.

This provocative argument has inspired practically an entire generation of paleontologists to test it with new evidence. But testing punctuated equilibria has turned out to be a challenge in itself. It demands dense fossil records that chronicle the rise of new species. Scientists have also had to develop sophisticated statistical tests to determine whether a pattern of change recorded in those fossils is explained best as stasis, a random walk, or directional change.

Scientists now have a number of cases in which evolution appears to unfold in fits and starts. **Figure 10.6** (top) comes from a study by Jeremy Jackson and Alan

Cheetham of bryozoans, small animals that grow in crustlike colonies on submerged rocks and reefs. On the other hand, more gradual, directional patterns of change have also emerged. **Figure 10.6** also charts the evolution of a diatom called *Rhizosolenia* that left a fairly dense fossil record over the past few million years. One structure on the diatom gradually changed shape as an ancestral species split in two.

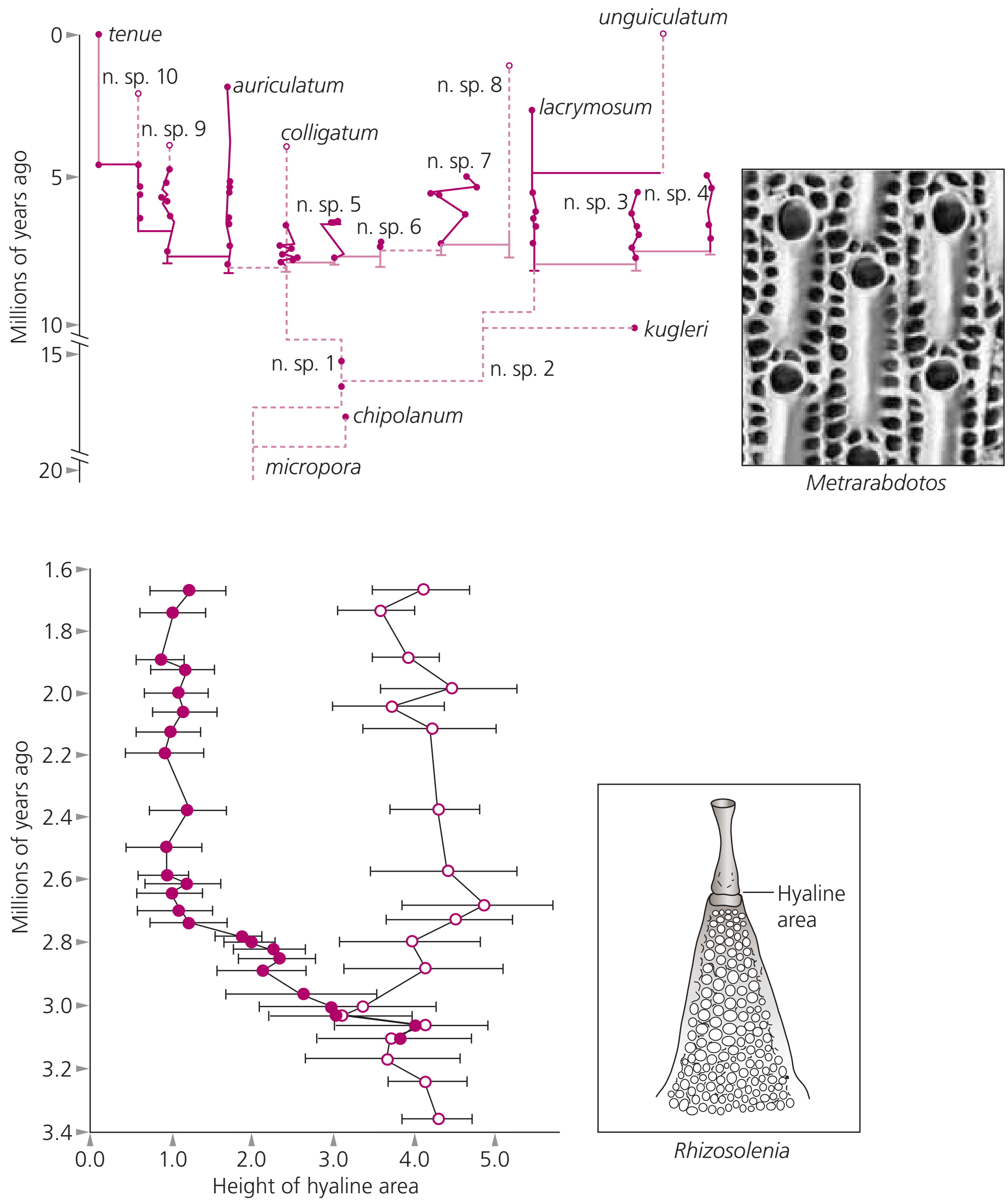


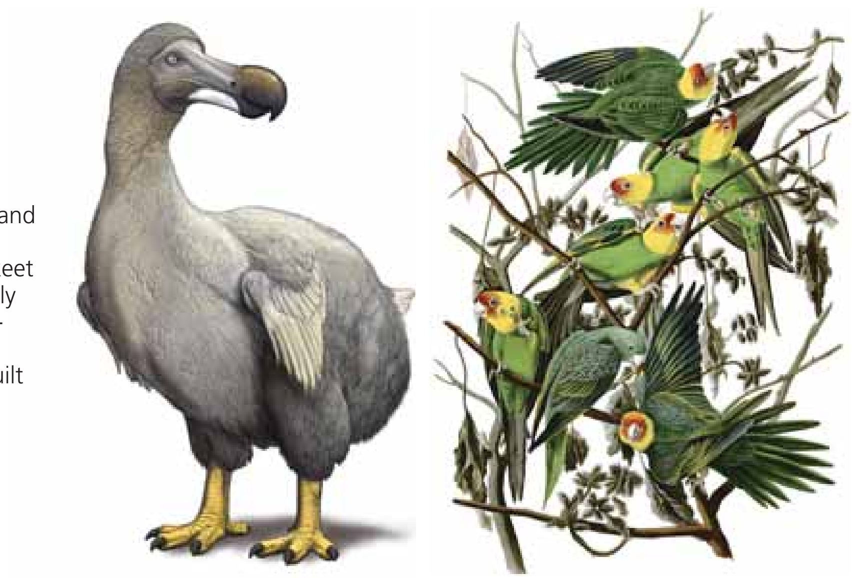
Figure 10.6 Paleontologists have documented cases of punctuated change and gradual change in the fossil record. Top: A lineage of bryozoans (*Metrarabdotos*) evolved rapidly into new species, but changed little once those species were established. Bottom: A shell-building organism called *Rhizosolenia* changed over the course of millions of years. This graph charts the size of a structure called the hyaline area. (Adapted from Benton, 2003)

At this point, paleontologists have found few well-documented cases that match the original model of punctuated equilibra, with rapid change happening only during speciation. But Eldredge and Gould's ideas have led to some significant changes in how paleontologists look at the fossil record. For example, Gene Hunt, a paleontologist at the Smithsonian Institution, recently developed a method for statistically analyzing patterns of change and used it to study 53 evolutionary lineages ranging from mollusks to fishes and primates. In 2007, Hunt concluded that only 5% of the fossil sequences showed signs of directional change. The other 95% was about evenly split between random walks and stasis. Hunt did not look for evidence of directional change during speciation, so he could not directly address the original model of punctuated equilibria. But Hunt's 2007 study does support the idea that stasis is a major feature of the history of life.

The Lifetime of a Species

Paleontologists estimate that 99% of all species that ever existed have vanished from the planet. To understand the process of extinction, paleontologists have measured the lifetime of species—especially species that leave lots of fossils behind. Mollusks (a group of invertebrates that includes snails and clams) leave some of the most complete fossil records of any animal.

Michael Foote, an evolutionary biologist at the University of Chicago, and his colleagues inventoried fossils of mollusks that lived in the ocean around New Zealand over the past 43 million years. They cataloged every individual fossil from each species, noting where and when it lived. Foote and his colleagues found that a typical mollusk species expanded its range over the course of a few million years and then dwindled away. **Figure 10.7** shows a selection of the species they cataloged. Some species lasted only 3 million years, while others lasted 25 million years.



Left: The dodo became extinct in the late 1600s, probably due to hunting and rats that ate their eggs. Right: The Carolina parakeet became extinct in the early 1900s, due in part to logging, which removed the hollow logs in which it built its nests.

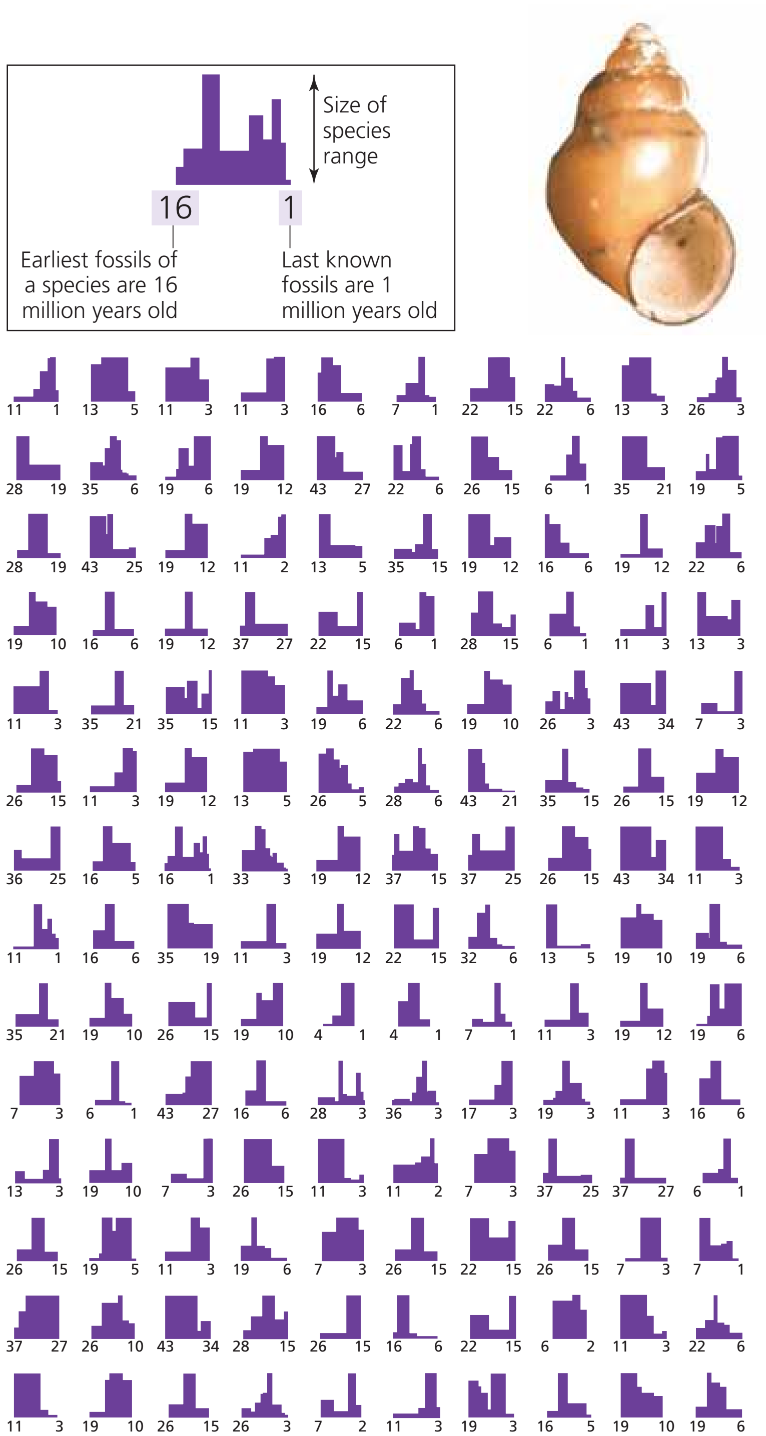


Figure 10.7 These graphs chart the rise and fall of mollusk species over the past 43 million years around New Zealand. The left number on each graph is the age of the earliest fossil in a species (in millions of years), and the right number is the age of the youngest fossil. The height of each graph represents the range over which fossils at each interval have been found. As these graphs demonstrate, some species survive longer than others, but in general they endured for a few million years. (Adapted from Foote, 2008)

To understand how species became extinct millions of years ago, biologists can get clues from extinctions that have taken place over the past few centuries. When Dutch explorers arrived on Mauritius in the 1600s, for example, they killed dodos for food or sport. They also inadvertently introduced the first rats to Mauritius, which then proceeded to eat the eggs of the dodos. As adult and young dodos alike were killed, the population shrank until only a single dodo was left. When it died, the species was gone forever.

Simply killing off individuals is not the only way to drive a species towards extinction. Habitat loss—the destruction of a particular kind of environment where a species can thrive—can also put a species at risk. The Carolina parakeet once lived in huge numbers in the southeastern United States. Loggers probably hastened its demise in the early 1900s by cutting down the old-growth forests where the parakeets made their nests in hollow logs.

Habitat loss can turn a species into a few isolated populations. Their isolation makes the species even more vulnerable to extinction. In small populations, genetic drift can spread harmful mutations and slow down the spread of beneficial ones. If the animals in an isolated population are wiped out by a hurricane, their numbers cannot be replenished by immigrants. As isolated populations wink out, one by one, the species as a whole faces the threat of extinction.

Cradles of Diversity

Understanding the long-term patterns of speciation and extinction may help scientists answer some of the biggest questions about today's patterns of biodiversity—such as why the tropics are so diverse. David Jablonski, a paleontologist at the University of Chicago, has tackled the question by analyzing the fossil record of bivalves, noting where they were located, how large their ranges became, and how long they endured.

Jablonski's analysis of 3,599 species from the past 11 million years revealed a striking pattern. Twice as many new genera of bivalves had emerged in the tropical oceans than had emerged in cooler waters. Jablonski found that once new bivalve genera evolved in the tropics, they expanded towards the poles. In time, however, the bivalves near the poles became extinct while their cousins near the equator survived. From these results, Jablonski argued that the tropics are both a cradle and a museum. New species can evolve rapidly in the tropics, and they can accumulate to greater numbers because the extinction rate is lower there as well. Together these factors lead to the high biodiversity of the tropics.

A similar pattern emerged when Bradford Hawkins, a biologist at the University of California, Irvine, studied the evolution of 7,520 species of birds. The birds that live closer to the poles belong to younger lineages than the ones that live in the tropics.

It's possible that the tropics have low extinction rates because they offer a more stable climate than regions closer to the poles. Ice ages, advancing and retreating glaciers, swings between wet and dry climates—all of these may have raised the risk of extinction in the cooler regions of the Earth. The changes that occurred in the tropics were gentler, which made it easier for species to survive. But the tropics also foster a higher rate of emergence of new species. Why the tropics can sustain more species than other regions is not clear, however; it's possible that the extra energy the tropics receive somehow creates extra ecological room for more species to live side by side.

Radiations

When biologists examine the history of a particular lineage, they discover a mix of diversification and extinctions. **Figure 10.8** shows the history of one such lineage, that of a group of mammal species called mountain beavers. About 30 species of mountain beavers have evolved over the past 35 million years in the

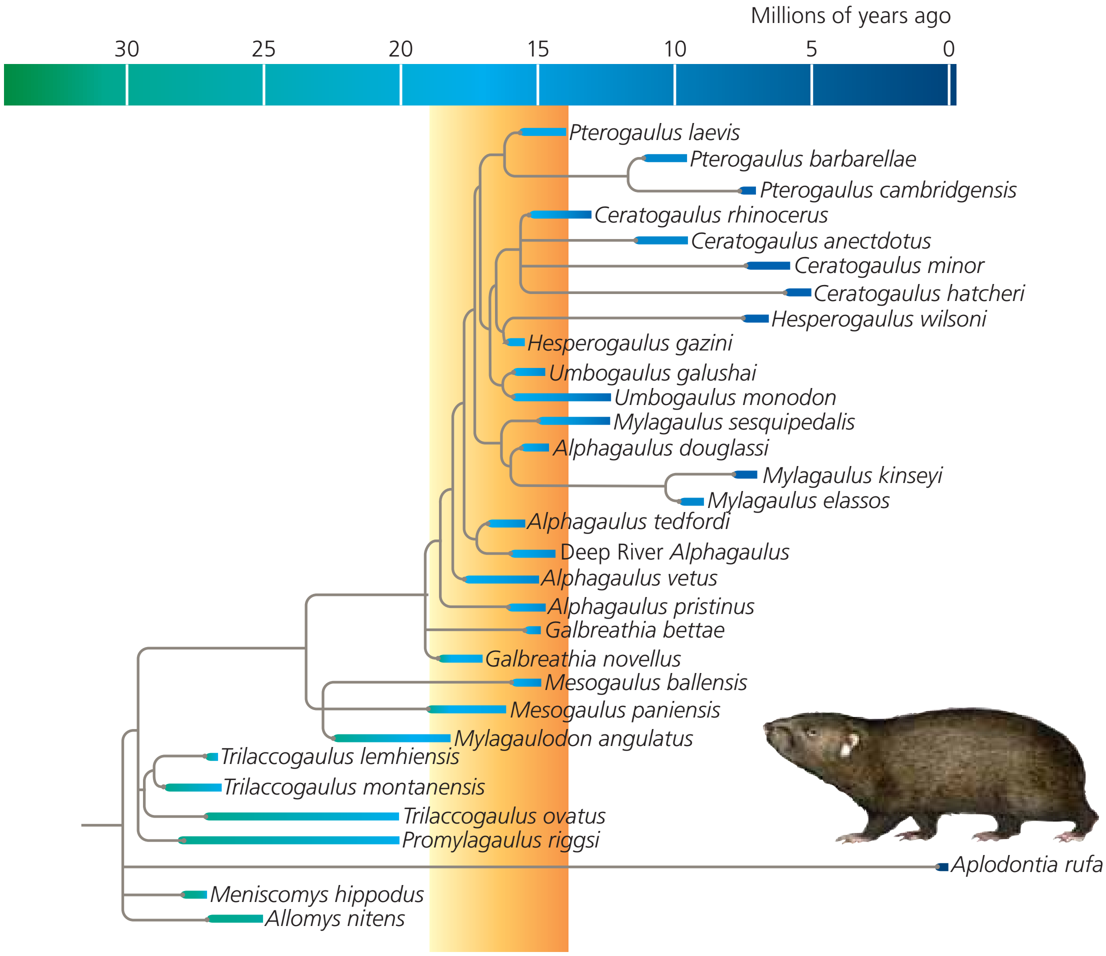


Figure 10.8 Over the past 35 million years, some 30 species of mountain beavers have existed in western North America. A burst of new lineages evolved around 15 million years ago. (Adapted from Barnovsky, 2008)

western United States, but today only a single species survives. Anthony Barnosky, a paleontologist at the University of California at Berkeley, and his colleagues have gathered fossils of mountain beavers, and they have found that new species of mountain beavers did not emerge at a regular pace. Instead, there was a period of rapid speciation around 15 million years ago. The number of mountain beaver species then gradually shrank as one species after another became extinct without new ones evolving to make up for their loss.

Sometimes a burst of diversification is accompanied by dramatic morphological evolution—an event known as an adaptive radiation. When the ancestors of Darwin's finches arrived on the Galápagos Islands a few million years ago, they did not simply evolve into 14 barely distinguishable species. They evolved distinctive beaks and behaviors that allowed them to feed on cactuses, crack hard nuts, and even drink the blood of other birds. The Great Lakes of East Africa also saw an adaptive radiation of cichlid fishes. These enormous lakes are geologically very young, in many cases having formed in just the past few hundred thousand years. Once they formed, cichlid fishes moved into them from nearby rivers. The fishes then exploded into thousands of new species. Along the way, the cichlids also adapted to making a living in a staggering range of ways—from crushing mollusks, to scraping algae and eating other cichlids.

Biologists don't yet know exactly what triggers adaptive radiations. One thing the African cichlids and Darwin's finches have in common is that they were able to move into a new ecosystem that was not already filled with well-adapted species. Without any established residents offering competition, the colonizers may have been able to evolve into a wide range of forms. Yet ecological opportunity cannot be the only factor behind adaptive radiations. Among the close rela-

Cichlid fishes that live in East Africa are a striking example of an adaptive radiation. Small founding populations entered each lake and then rapidly evolved into a wide range of forms and thousands of species.

tives of Darwin's finches are a lineage of birds that settled on the islands of the Caribbean. But they have only evolved into a narrow range of new sizes and shapes. It's possible that some lineages are somehow "preadapted" to take full advantage of ecological opportunity, while others are not.

A Gift for Diversity

Mountain beavers enjoyed a burst of new species 15 million years ago, but it's been pretty much downhill ever since. The story of insects is very different: they've enjoyed a durable success. They first evolved about 400 million years ago, and they've diversified fairly steadily ever since (**Figure 10.9**). The rise of insect diversity is all the more striking when you compare them to their closest relatives, a group of arthropods called entognathans that includes springtails.

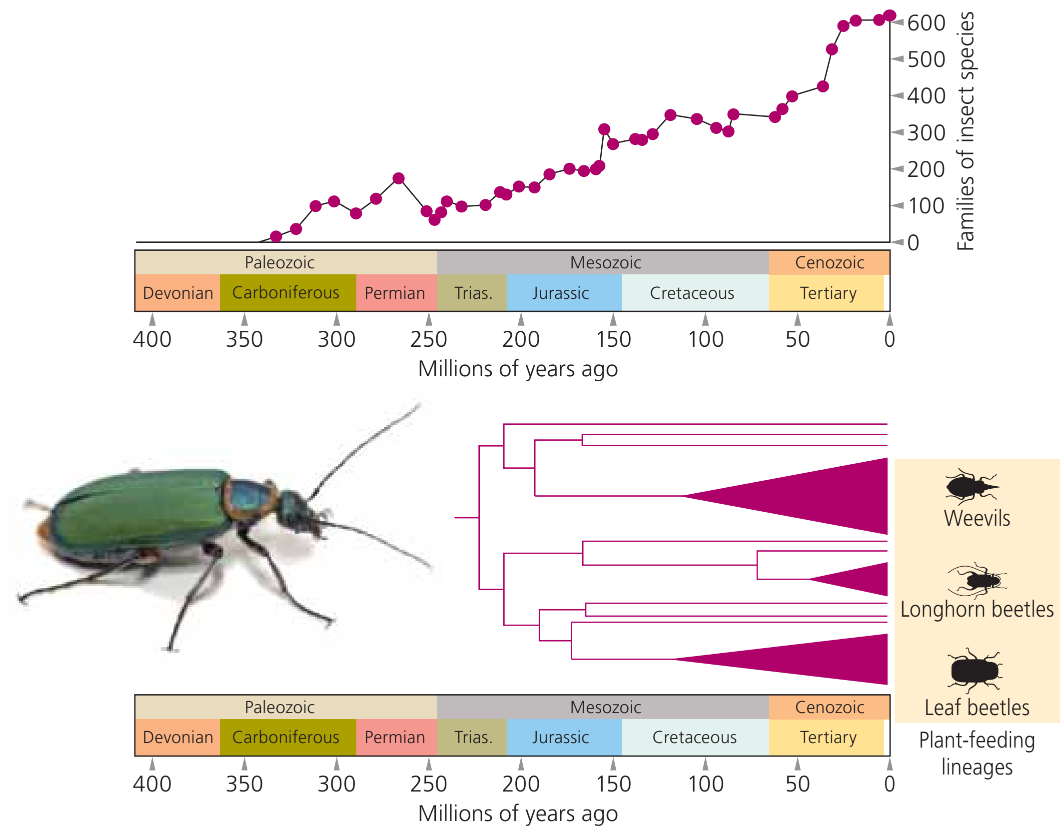


Figure 10.9 Insects are the most diverse group of animals on Earth. Top: Insect diversity has gradually grown over the past 400 million years. Bottom: Plant-feeding may have helped spur insect diversity, judging from the fact that many insect lineages that evolved the ability to eat plants became more diverse than their closest relatives. (Adapted from Mayhew, 2008, and Mayhew, 2009)

The entognathan lineage is just as old as the insect lineage. And while there are a million known insect species, there are only 10,600 entognathan species.

A number of biologists have probed the history of insects to determine what factors account for their huge diversity. Peter Mayhew, a biologist at the University of York, has tested the leading hypotheses. Insects don't seem to have a particularly high rate of speciation, he has found, but they do seem good at withstanding extinctions. Fifty percent of all families of insect species alive today existed 250 million years ago. None of the families of tetrapod species alive 250 million years ago exists today; all have been replaced by newer groups.

So what gives insects their sticking power? Mayhew argues that a few key factors are at work. The ability to eat plants provides insects with a huge amount of food; plant-eating has evolved several times among insects, and the plant-eating lineages tend to accumulate more species than closely related lineages of insects that don't eat plants. The small bodies of insects may lower the amount of food they need to survive, and shortens the time they need to develop from eggs. Wings also allowed insects to disperse much farther than arthropods that can only crawl or jump. Mayhew argues that all these advantages gave insects a massive edge, allowing them to colonize new habitats quickly and to survive catastrophes.

Lighting the Cambrian Fuse

By studying Darwin's finches and East African cichlids, scientists can get clues that help them understand much older, much bigger adaptive radiations. One of the biggest was the early rise of animals.

This period of animal evolution is sometimes nicknamed "the Cambrian explosion." Unfortunately, that name gives the impression that all the modern groups of animals popped into existence 540 million years ago at the dawn of the Cambrian period. Animals evolved from protozoans, which left fossils over a billion years before the Cambrian. Some 630 million years ago, one group of living animals—sponges—was already leaving behind biomarkers. By 555 million years ago, fossils belonging to some living groups began to appear—12 million years before the Cambrian Period.

The phylogeny of early animals is also showing how the body plans of living animals emerged not in a single leap, but in a series of steps. Arthropods, for example, have a body plan with a combination of traits (such as segments and an exoskeleton) seen in no other group of living animals. But some Cambrian fossils had some of those traits and not others. In **Figure 10.10**, we can see how these fossils help document the evolution of the arthropod body plan.

Clearly, then, animals did not drop to Earth in the Cambrian Period. They evolved. Nevertheless, the fossil record of the Cambrian chronicles a remarkable pulse of rapid evolution. When paleontologists look at 530-million-year-old rocks, they mainly find small, shell-like fossils. When they look at rocks just 20

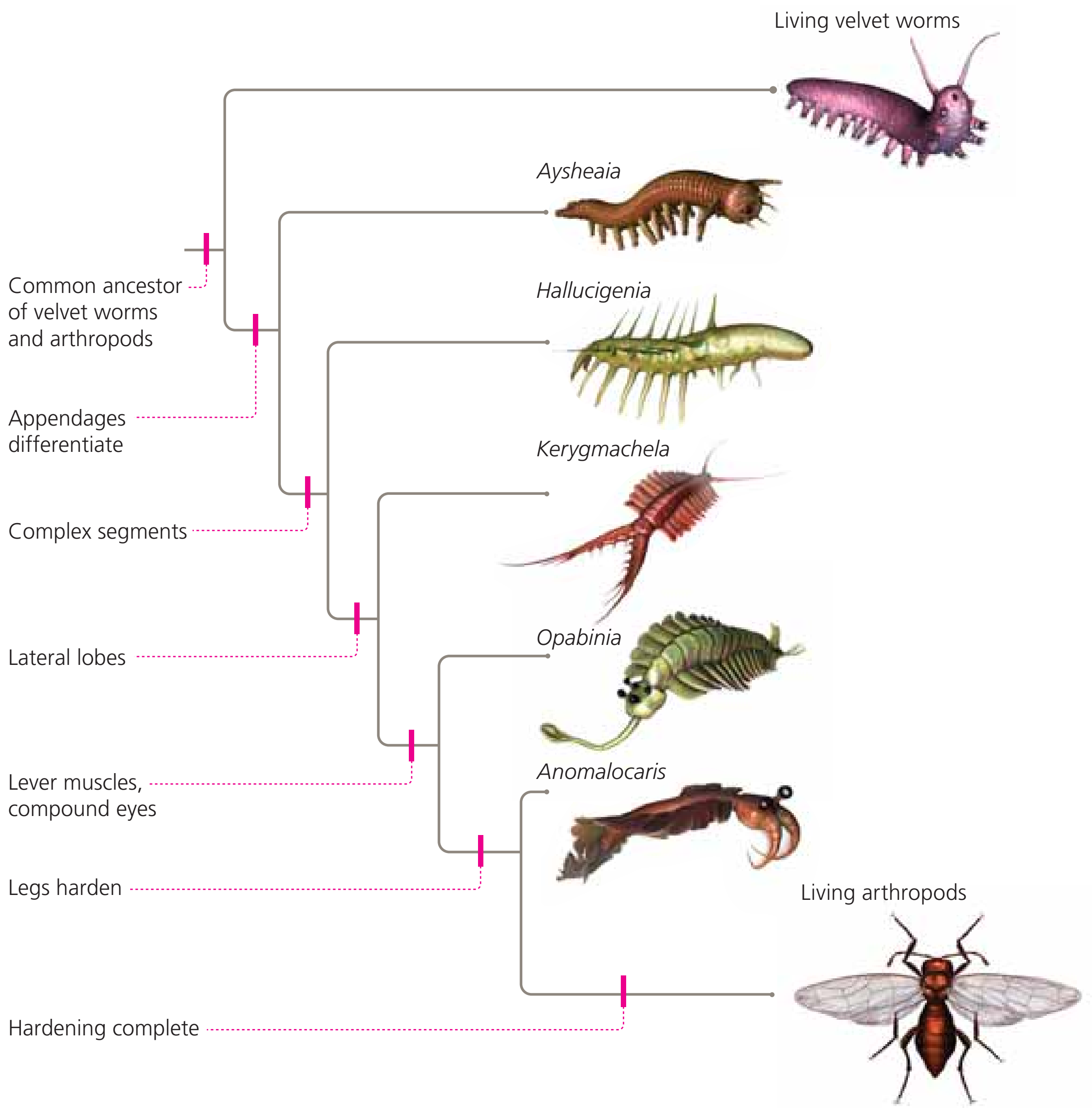


Figure 10.10 The fossil record documents how major groups of animals emerged during the Cambrian Period. Arthropods—a group that includes insects, spiders, and crustaceans—share a number of traits in common, such as jointed exoskeletons. Some Cambrian fossils belong to relatives of today's arthropods that lacked some of these traits. (Adapted from Budd, 2003)

million years younger, they find fossils that are recognizable relatives of living arthropods, vertebrates, and many other major groups of animals.

As an adaptive radiation, the early evolution of animals was unsurpassed. **Figure 10.11** is a diagram that marks the changes during the Ediacaran and Cambrian periods. One way to gauge these changes is to measure the diversity over time. **Figure 10.11** tracks diversity by tallying animal genera. Over the course of

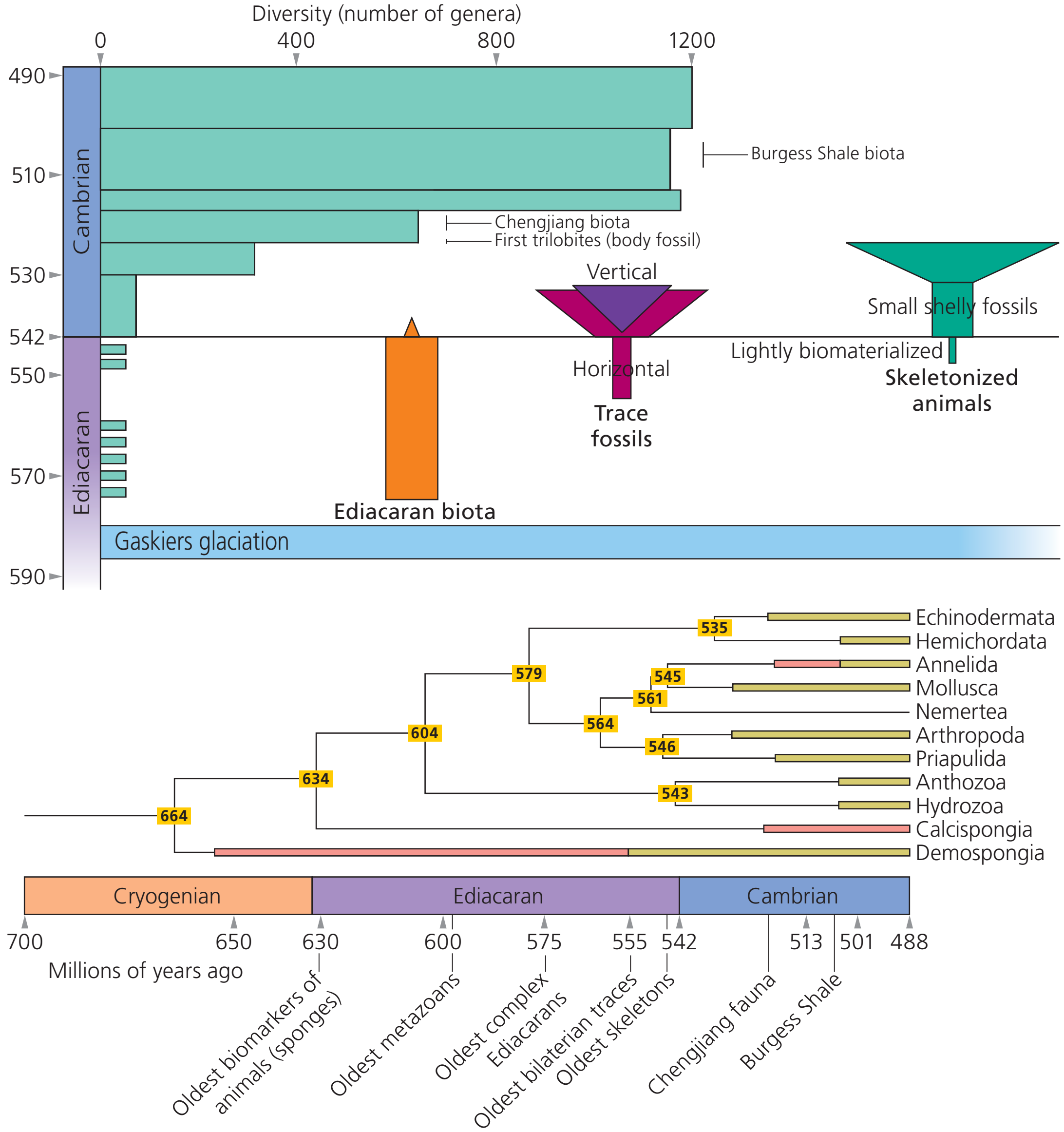


Figure 10.11 The early evolution of animals represents one of the biggest adaptive radiations in the history of life. Top: Fossils document the growing diversity of animals. Bottom: The major groups of animals evolved from common ancestors. Tan bars show the known fossil record of different groups. Pink bars show the range of fossils that have been proposed to belong to some groups. The numbers are ages based on DNA studies. (Top: adapted from Marshall, 2006. Bottom: adapted from Peterson, 2005)

about 40 million years, animal genera multiplied 100 times. But counting genera is not the only way to measure diversity. After all, there is much less variation among 100 genera of beetles than between a single species of squid and a single species of hummingbird. This morphological variation is known as disparity. The disparity of animals expanded rapidly during the Cambrian Period, before tapering off.

Paleontologists, developmental biologists, geochemists, and many other scientists are testing hypotheses that may explain this remarkable radiation. Some researchers observe that the radiation of animals came at a time when the Earth was going through some dramatic physical changes. It was emerging from a climate so cold that the entire planet was covered in glaciers. The ocean's chemistry was also changing drastically. For most of Earth's history, the oceans were almost devoid of free oxygen. While the atmosphere contained some free oxygen, the molecule could not survive for long in the ocean before bonding with other molecules. But Paul Hoffman of Harvard University and his colleagues have found evidence that oxygen levels began to rise in some parts of the ocean about 630 million years ago. By 550 million years ago, the change had spread across all of Earth's oceans.

Both the retreat of the glaciers and the rise of oxygen in the ocean may have spurred the rise of the animals. All animals need oxygen to fuel their metabolism and to build their tissues. The low levels of oxygen in the oceans may have made it impossible for the ancestors of animals to evolve into multicellular creatures.

If a rise in oxygen opened the door for animal evolution, what pushed the animals through? Part of that answer may lie within the animals themselves—in particular, in the set of genes that control their development. Most animal species alive today use the same "genetic tool kit" to build very different kinds of bodies (page 165). It was during the Ediacaran Period that this tool kit itself first evolved.

Douglas Erwin of the Smithsonian Institution argues that the animal tool kit allowed animals to evolve from a relatively limited number of Ediacaran forms to the frenzy of diversity that marked the Cambrian Period. As genetic circuits were rewired, new body parts evolved, along with new appendages, organs, and senses. It's possible that the genetic tool kit gave early animals the sort of flexibility adaptive radiations require.

The new body plans allowed animals to organize themselves into new ecosystems the Earth had never seen before. The earliest animals appear to have lived like sponges do today—trapping microbes or organic matter from the water as they remained anchored to the seafloor. But then animals evolved with guts and nervous systems, able to swim through the water or burrow into the muck. With their guts, they could swallow larger microbes, and, eventually, could even start to attack other animals. **Figure 10.12** shows a 550-million-year-old fossil *Cloudina* bearing the oldest known wounds from the attack of a predator.

Charles Marshall, a biologist at Harvard University, has proposed that the evolution of these new predators changed the fitness landscape for early animals. The old soft-bodied creatures anchored to the seafloor became easy targets for new predators. Now natural selection favored new defenses, such as hard shells, exoskeletons, and toxins. Predators in turn benefited from more sophisticated equipment for finding their prey, such as eyes. Their prey benefited from improved vision as well.

Natural selection did not converge on a single strategy for predators or for prey, Marshall argues. The new ecosystem created many different selection

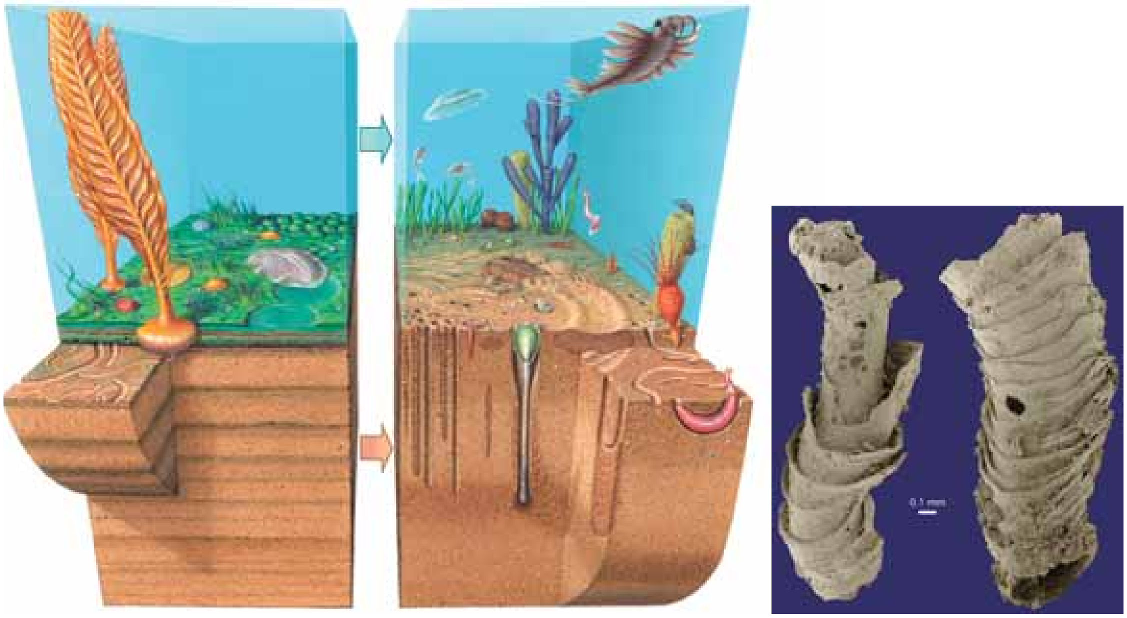


Figure 10.12 Left: During the Cambrian Period, the ecology of the ocean changed dramatically. New animals began burrowing, crawling on the ocean floor, and swimming rapidly after prey. Right: 550-million-year-old fossils bear holes bored by a predator—one of the earliest signs of predation in the fossil record.

pressures, each creating trade-offs with the other pressures. Instead of a single adaptive peak, Marshall proposes, animals now evolved on a fitness landscape erupting with a rugged expanse of hills. The complex landscape led to the extraordinary diversity and disparity of the animal kingdom.

Driven to Extinction

As new species emerged and evolved into disparate new forms, other species became extinct. And just as the origin of species and disparity form large-scale patterns, extinctions have formed patterns of their own. One of those patterns is illustrated in **Figure 10.13**. It shows how the extinction rate has gone up and down over the past 540 million years. A few pulses of extinctions stand out above the others. These mass extinctions were truly tremendous cataclysms. The biggest of all, which occurred 250 million years ago, claimed 55% of all genera. When scientists estimate the destruction in terms of species rather than genera, the event is even more catastrophic: perhaps 90% of all species disappeared. The fossil record also leaves ecological clues from that time that suggest that it was a period of global devastation. Forests and reefs drop out of the fossil record, and they do not reappear for 20 million years.

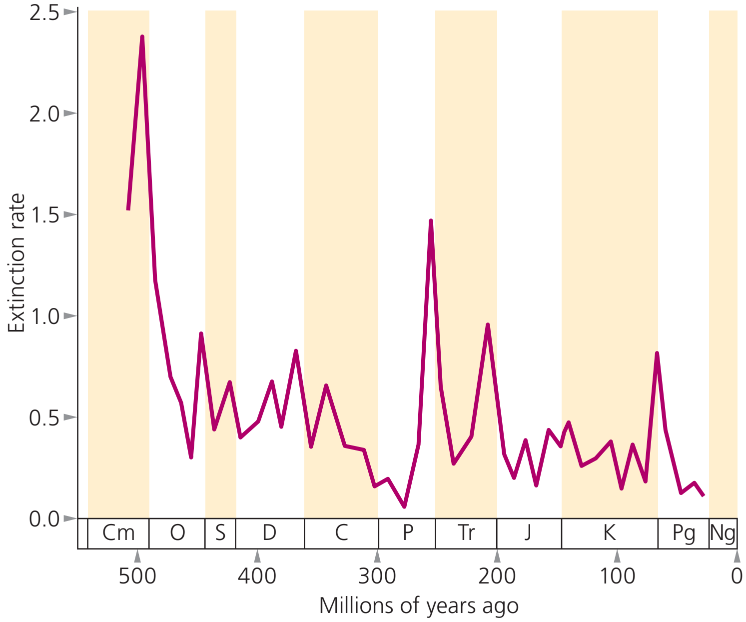


Figure 10.13 The rates at which species have become extinct has changed over time. The history of life has been marked by a few pulses of mass extinctions, in which vast numbers of species became extinct within a few million years. (Adapted from Alroy et al., 2008)

Only about 20% of all extinctions occurred during mass extinctions. The other 80% are known as background extinctions. For most individual species, scientists don't know the precise cause of extinction. But scientists can gather clues in the broad patterns of extinctions formed by thousands of species. In 2008, Jonathan Payne and Seth Finnegan, two paleontologists at Stanford University, surveyed 227,229 fossils of marine invertebrates from about 520 million years ago to 20 million years ago. They found that the bigger the geographical range of a genus, the longer it tended to survive. Small ranges raised the odds that a genus would become extinct.

One potential explanation for Payne and Finnegan's result is that a small range may make a genus more vulnerable to small-scale catastrophes, such as volcanic eruptions or an invasion by a dangerous predator. A small range may also be the mark of a genus that can survive only under very special conditions, such as a particular range of temperatures or a particular amount of rainfall. If the climate should change, the genus may not be able to adapt.

Another striking pattern in the history of life is the way in which major lineages gradually suffer extinctions as other lineages become more diverse. From 540 to 250 million years ago, the seafloor was dominated by invertebrates like trilobites and lamp shells (known as brachiopods), many of which fed by trapping bits of food suspended in the water. But today only a few hundred species of lamp shells survive, and trilobites disappeared entirely 252 million years ago. Now the seafloor is dominated by other animals, such as clams and other bivalves that bury themselves in the sediment.

Shannan Peters, a paleontologist at the University of Wisconsin, studies the shift from the old species (known as the Paleozoic Fauna) to the new ones (the Modern Fauna). Peters found that most fossils of the Paleozoic Fauna are found in sedimentary rocks known as carbonates, which formed from the bodies of microscopic organisms that settled to the seafloor. Most of the Modern Fauna fossils are found in rocks known as silicoclastics, which formed from the sediments carried to the ocean by rivers. Over the past 540 million years, carbonate rocks became rare, while silicoclastic rocks became common, possibly as rivers delivered more sediments to the oceans. Peters proposes that as the seafloor changed, the Modern Fauna could expand across a greater area, while the Paleozoic Fauna retreated to a shrinking habitat where it suffered almost complete extinction.

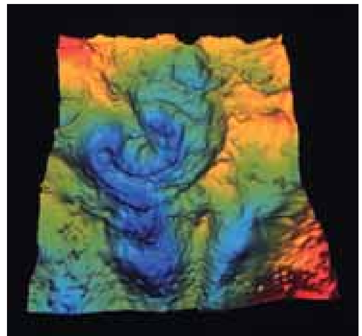
Another force influencing the extinction rate is the planet's changing climate. Geologists can estimate the average temperature in the distant past by measuring oxygen isotopes in rocks. High levels of oxygen-18 are a sign of a warm climate, because warm water can hold more of it than cold water. Peter Mayhew and his colleagues compared these climate records to the diversity of species over the past 300 million years. Diversity has gone down when the climate has been warm, Mayhew found, and it has been higher when the climate has been cool. The researchers found that most of the change was due to extinction rates going up rather than the speciation rate going down. As we'll see later, Mayhew's results are an ominous warning about our future.

When Life Nearly Died

Paleontologists have long debated whether mass extinctions shared the same causes as background extinctions, or whether some fundamentally different process was responsible. To test the alternative hypotheses, they have searched for rocks that formed during those mass extinctions that may chronicle those exceptional times.

In recent years researchers have discovered some new formations in China that record the mass extinctions at the end of the Permian in exquisite detail. These rocks are loaded with fossils from before, during, and after the mass extinctions, and they're also laced with uranium and other elements that geologists can use to make good estimates of their ages. The rocks indicate that these mass extinctions actually came in two pulses. The first pulse, a small one, came about 260 million years ago. Eight million years passed before the next one hit. The second strike was geologically swift—less than 300,000 years. How much less is a subject of debate; a few scientists have even proposed that it took just a few thousand years.

In Siberia, 252-million-year-old rocks reveal a potential culprit for the mass extinctions. They contain huge amounts of lava, spewed about by volcanoes. All

An asteroid struck the coast of Mexico 66 million years ago. It triggered giant tidal waves, vast forest fires, and a global environmental crisis. Right: Remnants of the crater have been found deep underground. Many researchers argue that the impact was at least partially responsible for mass extinctions at about the same time.

told, those eruptions covered a region as big as the United States. They released a harsh cocktail of gases into the atmosphere that would have disrupted the climate.

Atmospheric scientists have built computer simulations of the eruptions that suggest they could have devastated life in several ways. Heat-trapping gases, such as carbon dioxide and methane, could have driven up the temperature of the atmosphere. A warmer atmosphere could have warmed the oceans, driving out much of the free oxygen in the surface waters. Bacteria that thrive in low-oxygen water may have undergone a population explosion, releasing toxic gases such as hydrogen sulfide. Meanwhile, other gases released by the Siberian eruptions may have risen up to the stratosphere, where they could have destroyed the protective ozone layer. High-energy particles from space may have penetrated the lower atmosphere, creating damaging mutations. This chain of events could explain the puzzling appearance of deformed pollen grains during the Permian–Triassic extinctions.

Giant volcanic eruptions may not be the only things that can affect life across the planet. In the late 1970s, the University of California geologist Walter Alvarez was searching for a way to estimate precisely the ages of rocks. His father, the physicist Luis Alvarez, suggested that Walter measure levels of a rare element called iridium. Iridium falls to Earth from space at a relatively steady rate, and so it might act like a geological clock.

However, when Walter Alvarez collected rocks in Italy from the end of the Cretaceous Period 66 million years ago, he discovered concentrations of iridium far higher than average. The Alvarezes and their colleagues proposed that an asteroid or comet, rich in iridium, struck the Earth at the end of the Cretaceous

Period. In 1991, geologists in Mexico discovered a 110-mile-wide crater along the coast of the Yucatan Peninsula of precisely that age.

What made Alvarez's discovery electrifying for many paleontologists was the fact that the end of the Cretaceous also saw one of the biggest pulses of extinctions ever recorded. Through the Cretaceous, the Earth was home to giants. *Tyrannosaurus rex* and other carnivorous dinosaurs attacked huge prey such as *Triceratops*. Overhead, pterosaurs as big as small airplanes glided, and the oceans were dominated by whale-sized marine reptiles. By the end of the Cretaceous Period, these giants were entirely gone. The pterosaurs became extinct, leaving the sky to birds, which were the only surviving dinosaurs. Marine reptiles vanished as well. Along with the giants went millions of other species, from shelled relatives of squid called ammonites to single-celled protozoans.

The impact on the Yucatan may have had enough energy to trigger wildfires thousands of kilometers away and to kick up tidal waves that roared across the southern coasts of North America. It may have lofted dust into the atmosphere that lingered for months, blocking out the sunlight. Some compounds from the underlying rock in the Gulf of Mexico mixed with clouds to produce acid rain, while others absorbed heat from the sun to raise temperatures.

Many researchers argue that this impact was in large part responsible for the mass extinctions at the end of the Cretaceous Period. But some geologists point out that, not long before the impact, India began to experience tremendous volcanic activity that probably disrupted the atmosphere and the climate as well. Meanwhile, some paleontologists question how much effect the impact or the volcanoes had on biodiversity at the end of the Cretaceous. The diversity of dinosaurs and other lineages was already dropping millions of years earlier. Moreover, if a sudden environmental cataclysm wiped out the dinosaurs and millions of other species, it's strange that snakes, lizards, turtles, and amphibians did not also suffer mass extinctions. Those are the animals that today are proving to be exquisitely vulnerable to environmental damage.

Whatever the exact causes of mass extinctions turn out to be, it is clear that they left great wakes of destruction. After the Permian–Triassic extinctions 252 million years ago, for example, forests were wiped out, and weedy, fast-growing plants called lycopsids formed vast carpets that thrived for a few million years before giving way to other plants. And when ecosystems finally recovered from the mass extinctions, they were fundamentally different than before. On land, for example, ancient reptile-like relatives of mammals were dominant before the extinctions. They took a serious blow, however, and did not recover. Instead, reptiles became more diverse and dominant—including dinosaurs, which would thrive for 200 million years.

A similar pattern unfolded 66 million years ago, with the Cretaceous extinctions. After large dinosaurs became extinct, mammals came to occupy many of their niches, evolving into large carnivores and herbivores. In the oceans, mammals evolved into whales, taking the place of marine reptiles (page 8). Even as mass extinctions wipe out old biodiversity, they may open the way for the evolution of new radiations, either by wiping out predators or by clearing out ecological niches.

The New Die-off

The dodo was not alone as it headed for oblivion. Other species were also being driven extinct by humans at the same time. There are written accounts of a few hundred species that have become extinct, but scientists suspect that many others have also quietly vanished. Some scientists have tried to estimate the current rate of extinctions by focusing on groups of species that have enjoyed a lot of scientific scrutiny. Birds are one such group, because they're relatively big, bright, and adored by bird-watchers around the world.

In 2006, Stuart Pimm of Duke University, an expert on bird extinctions, tallied up the total number of bird extinctions known to have been caused by humans. He looked at historical records of birds such as the dodo, but he also included extinct birds discovered by archaeologists on islands in the Pacific Ocean. Pimm and his colleagues calculated how quickly birds were becoming extinct and compared this to background rates of extinction documented in the fossil record. They concluded that birds are disappearing 100 times faster. And Pimm warns that this rate will only accelerate in the coming decades. Many bird species that aren't extinct are already endangered, their populations vanishing thanks to hunting and lost habitat. Given the growing human population and the

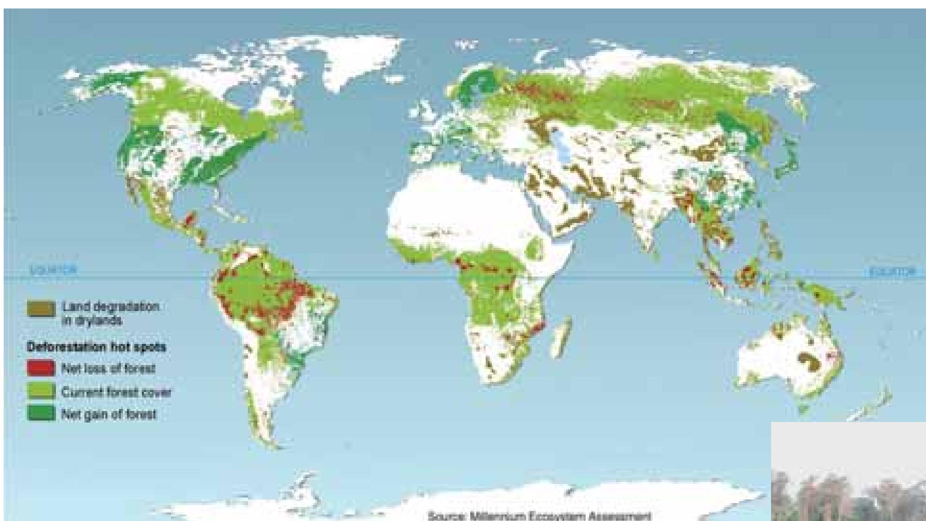


Figure 10.14 Humans have had a major impact on most of the world's habitats. Millions of acres of tropical rain forest are being cut down for timber and to clear land for farming. (Adapted from Millennium Ecosystem Assessment, 2005)

continuing deforestation (**Figure 10.14**) in many bird habitats, Pimm fears that these endangered species will become extinct as well. He predicts that, in a few decades, birds will become extinct 1,000 times faster than the background rate.

Other scientists have come up with equally grim predictions for other groups of animals and plants (**Figure 10.15**). These studies indicate that we are entering a new phase of mass extinctions on a scale not seen for 66 million years. And these studies were carried out before researchers began to grapple with another major threat to biodiversity: the release of carbon dioxide from fossil fuels.

Every year, humans release more than seven billion metric tons of carbon dioxide into the atmosphere. Over the past two centuries, humans have raised the concentration of carbon dioxide in the air from 280 parts per million in 1800 to 383 parts per million (**Figure 10.16B**). Depending on how much coal, gas, and oil we burn in the future, levels of carbon dioxide could reach 1,000 parts per million in a few decades.

This extra carbon may have two kinds of devastating effects. Carbon dioxide entering the oceans is making the water more acidic. James Zachos of the University of California, Santa Cruz, and his colleagues have studied the effects of acidic ocean water on animal life. They find that it interferes with the growth of coral reefs and shell-bearing mollusks, such as snails and clams. These animals may simply die and the reefs may disintegrate. The collapse of coral reefs could lead to more extinctions, because they serve as shelters for a quarter of all marine animal species.

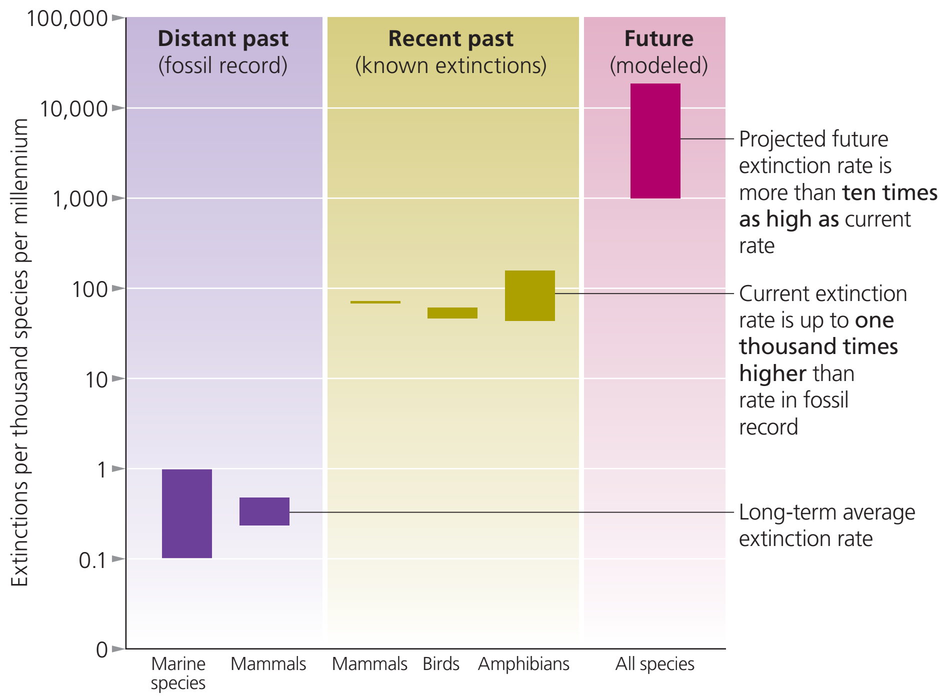


Figure 10.15 The rate of extinction is now much higher than the historical background rate. If it increases, as many scientists now predict, we are entering a new pulse of mass extinctions. (Adapted from Millennium Ecosystem Assessment, 2005)

Carbon dioxide has another effect on life: it warms the atmosphere by trapping the heat from the Sun (**Figure 10.16A**). The average global temperature has already risen 0.74 degrees Celsius (1.33 degrees Fahrenheit) over the past century (**Figure 10.16C**).

Over the next century, computer models project, the planet will warm several more degrees unless we can slow down the rise of greenhouse gases in the atmosphere. Animals and plants have already responded to the change. Thousands of species have shifted their ranges. Some species now live beyond their historical ranges, tracking the climate to which they've adapted. Other species that live on mountainsides have shifted to higher elevations.

The effects of climate change on biodiversity in the future are far from clear, but many scientists warn that they could be devastating. Among the first victims

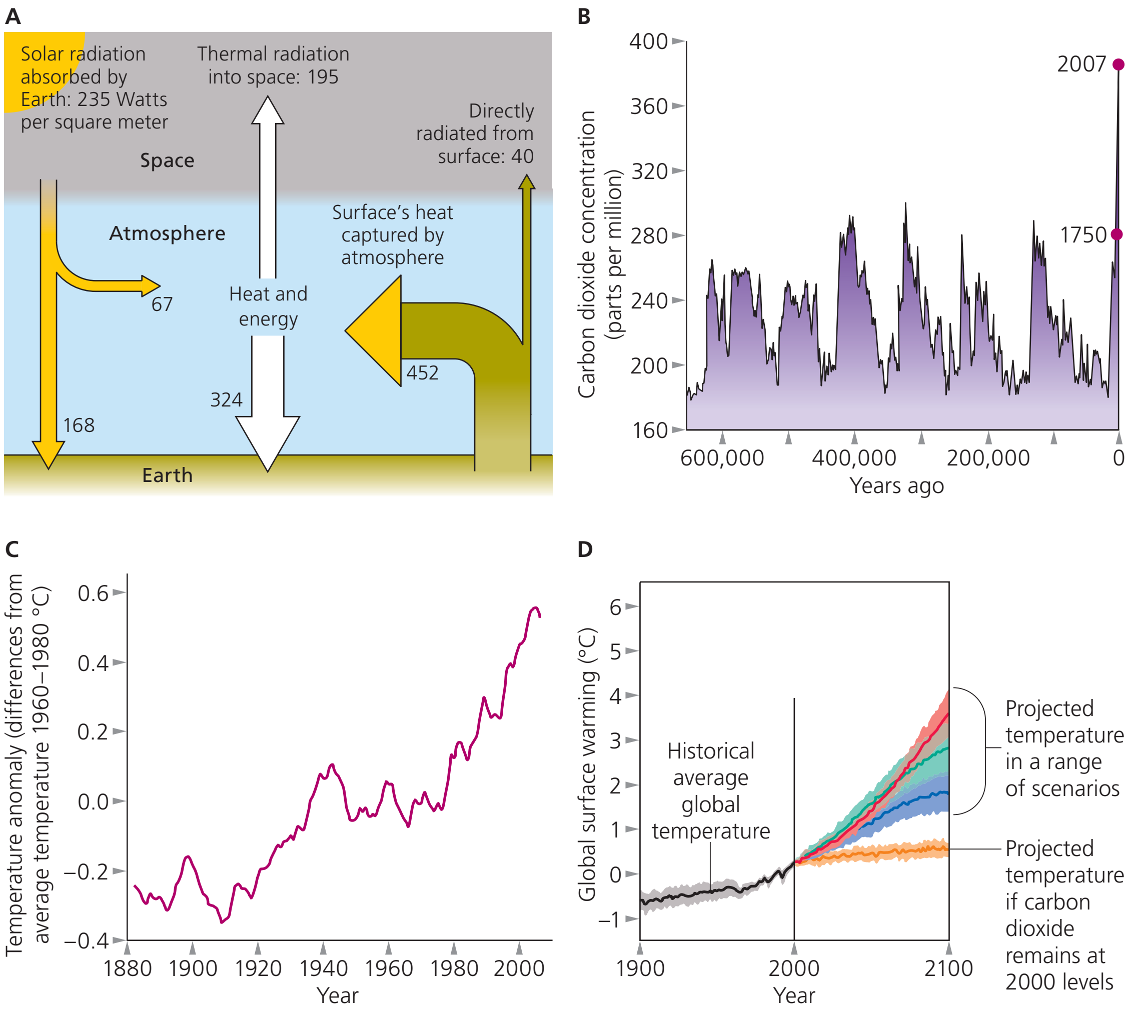


Figure 10.16 Carbon dioxide traps heat in the atmosphere, raising the planet's temperature. Humans are dramatically increasing the concentration of carbon dioxide. The rising temperature may lead to the extinction of many species.

of climate change may be mountain-dwelling species. As they move to higher elevations, they will eventually run out of refuge. In northern Australia, for example, the rare white lemuroid possum has only been found living on mountainsides at elevations higher than 1000 meters. In 2008 Australian biologists could not find a single possum and fear that it has become the first mammal to be driven extinct by manmade global warming. Polar bears and other animals adapted to life near the poles may also see their habitats simply melt away. In other cases, the climate envelope will shift far away from its current location. Some species may be able to shift as well, but many slow-dispersing species will not. Conservation biologists are now debating whether they should plan on moving species to preserve them.

It is reasonable to ask why we should care about these coming mass extinctions. After all, extinction is a fact of life, and life on Earth has endured through big pulses of extinctions in the past, only to rebound to even higher levels of diversity.

Mass extinctions are a serious matter, even on purely selfish grounds. People who depend on fish for food or income will be harmed by the collapse of coral reefs, which provide shelter for fish larvae. Bees and other insects pollinate billions of dollars of crops, and now, as introduced diseases are threatening to wipe them out in the United States, farmers will suffer as well.

Biodiversity also sustains the ecosystems that support human life, whether they are wetlands that purify water or soil in which plants grow. A single species can disappear without much harm to an ecosystem, but the fossil record shows that extinctions can lead to the complete collapse of ecosystems for millions of years. Paul Ehrlich, an evolutionary biologist at Stanford University, likens the process to someone popping rivets from a plane in flight. One or two rivets may go missing without causing trouble, but, eventually, taking away yet another rivet leads to an abrupt crash.

Coral reefs, which support much of the biodiversity of the ocean, are suffering from pollution and overfishing. As levels of carbon dioxide rise, they face further damage from the acidification of sea water.

Evolution has also generated many molecules that have enormous economic value. Antibiotics are produced by fungi and bacteria, for example. Snake venom has been adapted to treat blood pressure. The enzymes made by archaea in hot springs are now used to rapidly make copies of fragments of DNA in laboratories. Many potentially valuable molecules are waiting to be discovered. In 2007, Scott Strobel, a molecular biologist at Yale University, took 15 undergraduates on an expedition to a rain forest on the border of Bolivia and Peru. There they collected fungi and bacteria from plants and took them back to Yale to analyze. On that single field trip, the students gathered 135 species, many of which were only distantly related to any known lineage of bacteria or fungi. Strobel's students tested 88 of the new species and found that 65 of them contained molecules that could stop the growth of disease-causing microbes. If the plants on which they live become extinct, these fungi and bacteria may become extinct along with them. With every species that becomes extinct, we lose more of the raw material for essential industries ranging from biotechnology to chemical engineering to medicine.

Moreover, as species become extinct, we lose the opportunity to learn about our own evolutionary history. All of the great apes—our closest living relatives—are endangered, as they are hunted for food and driven out of forests that are being logged or cleared to make way for plantations. As we'll see in Chapter 14, some of the most important discoveries about how our own species evolved language, culture, reasoning, and even consciousness came from comparisons with those cousins now on the edge of extinction.

TO SUM UP...

- **Biogeography is the study of the distribution of species around the world.**
- **Species can move from where they originated to continents and islands. This process is known as dispersal.**
- **As continents split and drift, they can carry species with them. This process is known as vicariance.**
- **Lineages can produce new species at fast or slow rates. Lineages can also experience stasis and bursts of change.**
- **Species on average last a few million years before becoming extinct.**
- **Extinction can be caused by predation, loss of habitat, or other factors that reduce a species' population.**
- **One hypothesis for the diversity in the tropics is that the region fosters the origination of new species and allows species to last longer.**
- **Adaptive radiations are rapid diversifications of lineages.**
- **Some lineages are more diverse than others. Insects appear to be more diverse because insect species are less likely to become extinct.**
- **The early evolution of animals was a major adaptive radiation, possibly triggered by worldwide environmental changes. The struggle between predators and prey accelerated the diversification of animal lineages.**
- **The extinction rate has varied over time. On at least three occasions, there have been mass extinctions.**
- **Periods of high extinction rates coincide with major environmental changes, including asteroid impacts, volcanic eruptions, and global warming.**
- **Humans are the agents of a new pulse of extinctions.**