14 Macroevolution

The Long Run

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Learning Objectives

- Compare and contrast the processes involved in macroevolution and microevolution and the patterns that result from these processes.
- Evaluate the effects on total species diversity when origination and extinction rates vary.
- Evaluate the kinds of evidence needed to distinguish between dispersal events and vicariance events in the fossil record.
- Explain how paleontologists analyze the fossil record to reconstruct macroevolutionary patterns.
- Explain what an adaptive radiation is and what kinds of opportunities can give rise to adaptive radiations.
- Compare background extinctions with mass extinctions, and provide an operational definition of mass extinction.
- Describe two abiotic factors potentially responsible for mass extinctions.
- Evaluate the evidence for human influence on biotic and abiotic factors affecting biodiversity, and discuss whether those influences may lead to another mass extinction.

Anthony Barnosky can often be found in a cave, searching for fossils. He's spent decades unearthing bones of North American mammals that lived during the Pleistocene, from 2.6 million years ago to 11,700 years ago, and he has found the bones of everything from rodents to giant mastodons. But for Barnosky, who teaches at the University of California, Berkeley, the fossils he *doesn't* find are just as interesting as the ones that he does find. Barnosky and his colleagues use their fossils to track the history of species through time, observing how new species emerge in the fossil record. And when they stop finding fossils in younger rocks, they get clues about how those species became extinct.

The world today is home to a mind-boggling number of species. Scientists have named about 1.8 million species, but according to a recent estimate, 8.7 million species in total may exist on Earth (Mora et al. 2011). Even that figure is an underestimate, because it doesn't take into account the emerging picture of microbial diversity (Chapter 13). There can be 10,000 species of microbes in a single spoonful of soil, and potentially hundreds of millions of microbial species worldwide. But over the past 3.5 billion years, many other species have come

◄ As recently as 12,000 years ago, North America was home to a wide range of large mammals such as this saber-toothed tiger (*Smilodon fatalis*) and giant bison (*Bison latifrons*). These and many other species of large North American mammals have become extinct, due at least in part to the arrival of human hunters on the continent.

into existence and then disappeared. Paleontologists like Barnosky (**Figure 14.1**) gather the clues we can use to understand the history of biological diversity.

By estimating the ages of the earliest and youngest fossils of species, paleontologists can measure the lifetime of species. Barnosky and his colleagues find that the saber-toothed lions, rhinoceroses, and other Pleistocene mammals they uncover typically endure for a million years or more. Other paleontologists have tracked the lifetimes of species of other organisms, ranging from insects to mosses. Some species last a long time; others disappear after much less time. But roughly speaking, a million years is a pretty good estimate of the average lifetime of a species.

We can use the lifetime of species to estimate how many species have ever existed. Since there are some key factors about evolution that we don't know precisely, we'll have to make some reasonable assumptions when developing our estimate. To begin with, let's assume that before each species died off, it produced a daughter species that also endured for a million years. To avoid overestimating the number of extinct species, we'll also assume that species diversity at the start of the Cambrian, 540 million years ago, was only 10 percent of what it is now. We'll also assume that species diversity has been increasing steadily ever since to its current level. To model this increase in diversity, we'll assume that it increased at increments of 1 percent (so over the course of 540 million years, each 1 percent jump in species diversity would take 6 million years).

If you use these assumptions to add up the numbers of species that lived and died at every million-year interval over the past 540 million years, you get a total number of extinct species that vastly outnumbers the species alive today—by about a factor of 297. In other words, the number of species alive today is only about one-third of 1 percent of all species that have lived since the Cambrian. And because this is a conservative model, we can say that *at least* 99.67 percent of all species in the history of life have become extinct.

The large-scale processes and patterns of evolution—such as changes in levels of biological diversity—are known as **macroevolution**. The term stands in contrast to **microevolution**, the change of allele frequencies within populations caused by mechanisms such as genetic drift and natural selection. As we saw in Chapter 6, microevolution occurs on such a small scale that scientists can observe it in wild populations and conduct experiments to test evolutionary hypotheses. Scientists cannot observe macroevolution as closely, for the simple reason that they don't live for millions of years. Instead, they study macroevolution by exploring the evidence left behind—either in the fossil record, in the genetic patterns revealed through molecular phylogenetics, or in the current distribution of living species.

In this chapter, we'll explore the methods scientists use to study macroevolution and the insights they've gleaned from it. We will begin with the geographic patterns of macroevolution—why certain clades are found only in some parts of the world, for example, or why some regions have more species than others. Macroevolution produces patterns through time as well as space; we'll look at how scientists measure the rates of origination and extinction in the fossil record and examine the causes of changes in global biodiversity. We will consider the factors that drive some clades to diversify into many new species while other clades remain species-poor (**Figure 14.2**).

Figure 14.1 Anthony Barnosky of the University of California, Berkeley, explores caves with his colleagues to reconstruct the changing biodiversity of North America over the past 30 million years.

Macroevolution is evolution occurring above the species level, including the origination, diversification, and extinction of species over long periods of evolutionary time.

Microevolution is evolution occurring within populations, including adaptive and neutral changes in allele frequencies from one generation to the next.

Macroevolution also includes abrupt drops in diversification rates caused by the rapid extinction of many species. These extinction pulses offer a sobering warning for our own future. As we'll see in this chapter, the research of scientists like Barnosky has revealed that we humans are driving species extinct at a worrying rate, a rate that could potentially increase to truly catastrophic levels in the years to come. •

14.1 Biogeography: Mapping Macroevolution

When we look at the diversity of life across the planet, certain patterns jump out. Some regions of the world, such as the tropics, are more species-rich than others (**Figure 14.3**). Certain groups of species are common in some places and rare in others. Marsupial mammals, for example, are mostly found in Australia, whereas other regions of the world have much lower levels of marsupial diversity.
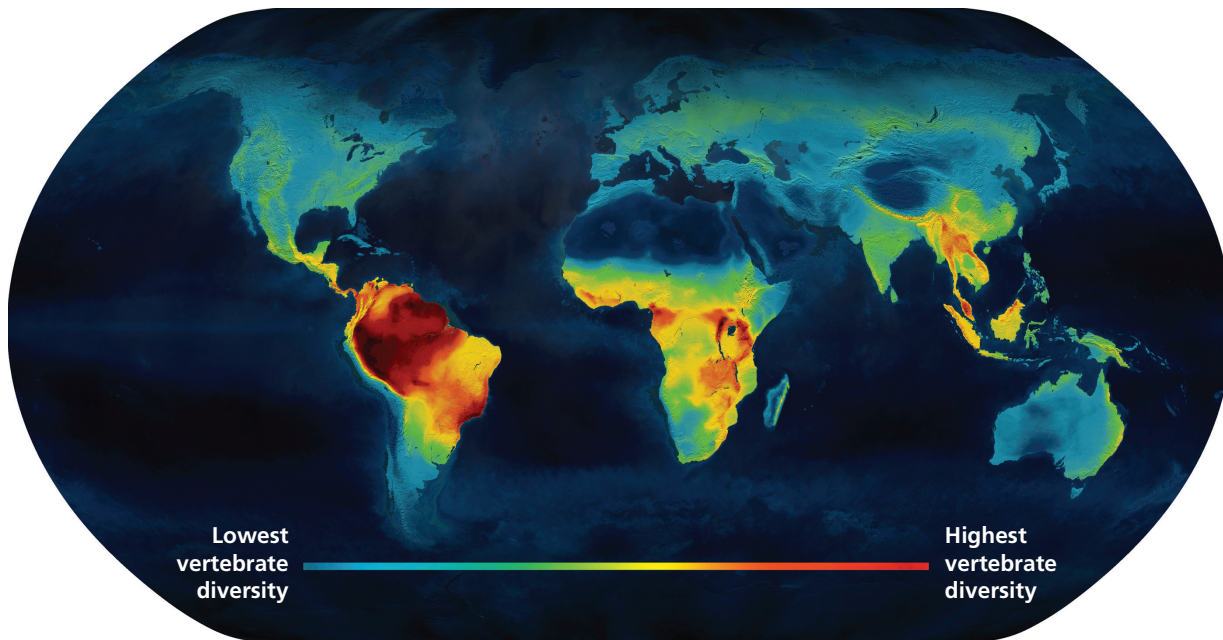
The study of these patterns is known as **biogeography**. Before the nineteenth century, many naturalists assumed that biogeographic patterns existed because the Creator had chosen to put species in places to which they were well adapted. But in his travels aboard the *Beagle*, Darwin observed many serious flaws in this explanation (Chapter 2). Environmental conditions such as climate alone could not completely account for the distribution of species. Llamas can live in the Andes, for example, so it doesn't make sense that they aren't found in the Rockies as well.

Darwin also observed that environmental conditions often failed to explain the similarities among groups of species. The rodents that live on South American mountains showed many signs of being closely related to the rodents that live on the South American plains—as opposed to the rodents of the environmentally similar mountains of North America. Darwin argued that an adaptive divergence had occurred

Figure 14.2 There are an estimated 300,000 species of beetles. Their high diversity is the result of an origination rate notably higher than their extinction rate.

Biogeography is the study of the distribution of species across space (geography) and time.

Figure 14.3 The tropics have higher levels of biological diversity. This map shows levels of vertebrate diversity. Some scientists have proposed that the tropics are rich in species because of the high speciation rate there. Others have argued that extinction rates are low. It's possible a combination of factors is responsible.
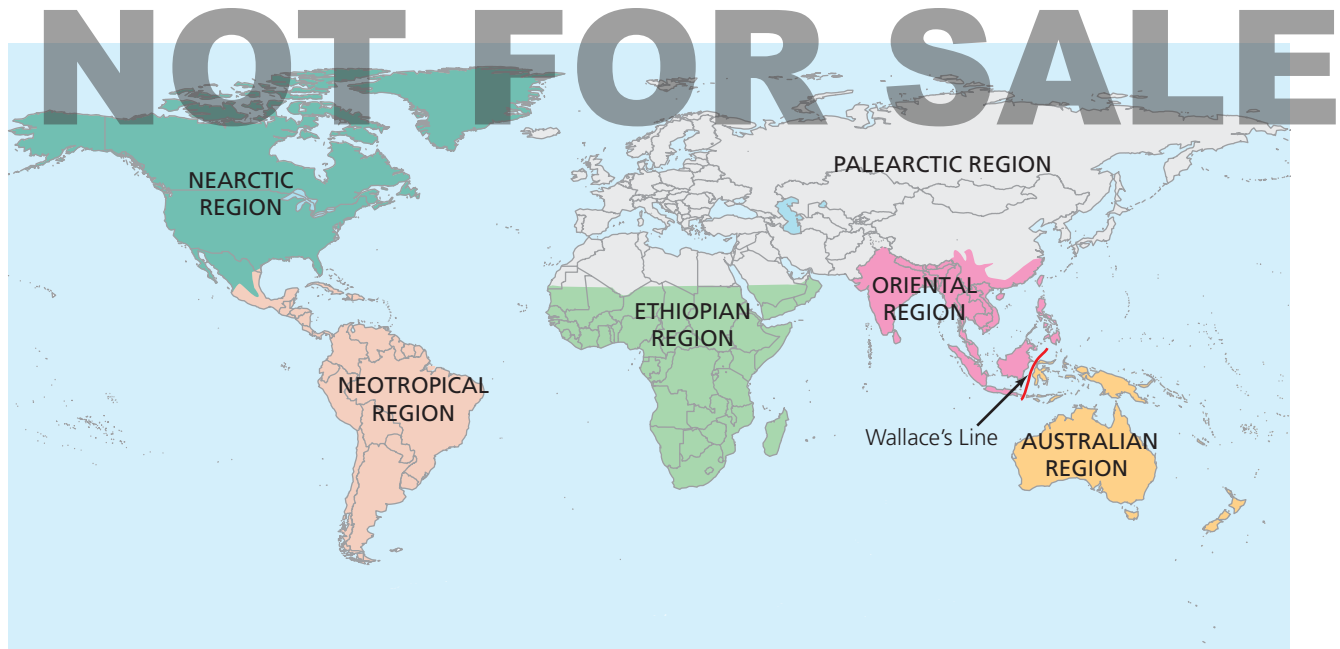
Lowest vertebrate diversity

Highest vertebrate diversity

NEARCTIC REGION

PALEARCTIC REGION

ORIENTAL REGION

ETHIOPIAN REGION

NEOTROPICAL REGION

Wallace's Line

AUSTRALIAN REGION

Figure 14.4 Alfred Russel Wallace drew the first global map of biogeographical regions.

among the rodents of South America and that contiguous populations of rodents survived in each particular environment.

When Darwin traveled to islands, he could see that those ecosystems were dominated by species that were good dispersers. They were home to many species of bats and birds, for example, but few amphibians or elephants. This distribution of island species made sense as the result of species colonizing the islands from the mainland and then adapting to those habitats.

Alfred Russel Wallace, co-discoverer of evolution by natural selection, also made important observations about biogeography. He separated the world into six major biogeographical provinces, each one having its own distinctive balance of species (**Figure 14.4**). The boundary between two of these provinces—southeast Asia on one side and Australia and New Zealand on the other—is particularly striking. It actually runs through the middle of the Indonesian Archipelago. Islands on both sides of the boundary have very similar environments but very different species assemblages. The science of biogeography seeks to explain such intriguing patterns of species distribution.

Dispersal describes the movement of populations from one geographic region to another with very limited return exchange, or none at all.

When Darwin and Wallace first investigated biogeography, the only way they could envision species getting to where they are now was through **dispersal**. Birds flew to islands; elephants walked over mountain ranges; seeds were carried by water to distant shores. But dispersal fell short in explaining some patterns of biogeography—why, for example, marine invertebrates on the east and west coasts of Panama are so remarkably similar (a shrimp today would have to swim all the way around the continent of South America to get from one of these populations to the other). As geologists learned more about how the surface of the Earth changes, it became clear that the formation of barriers to migration and gene flow can also shape biogeographic patterns (Chapter 13). This process is known as **vicariance**.

Vicariance is the formation of geographic barriers to dispersal and gene flow, resulting in the separation of once continuously distributed populations.
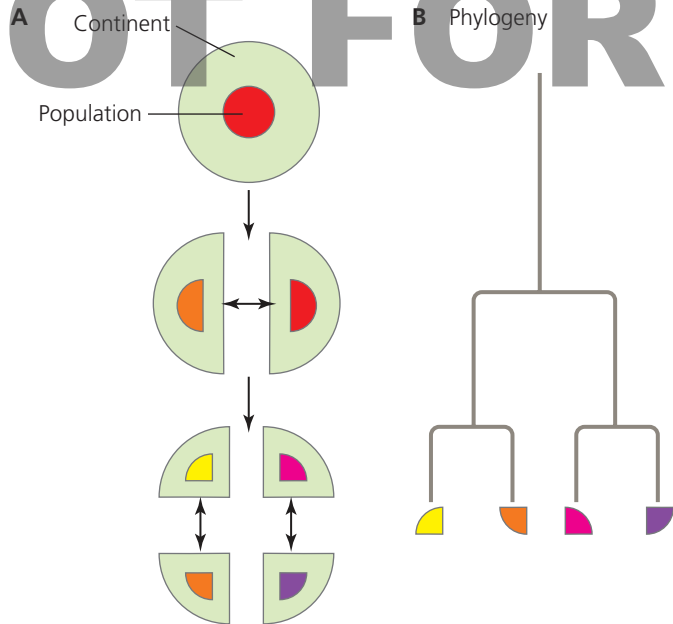
Many geological processes can drive vicariance. Rising sea levels can turn peninsulas into islands. Mountain ranges can rise up, splitting a population. Rivers can suddenly change course. Continents can break up and drift apart. **Figure 14.5** shows a hypothetical example of vicariance. A continent breaks in two, and those two landmasses split in turn. If a clade does not disperse during this breakup, its phylogeny should reflect the history of the landmass. The most closely related clades should be found on the most recently separated landmasses.

The history of marsupials is a spectacular example of how both vicariance and dispersal produce complex patterns of biodiversity. Although most living species of marsupials are found today in Australia, the oldest marsupial fossils come from

A Continent

Population

B Phylogeny

China and North America. Yet there is only one species of marsupial in all of North America today (the Virginia opossum), and none at all in China. How did we get to this puzzling situation?

We can understand this pattern by integrating several separate lines of evidence: from studies on the molecular phylogeny of living marsupials, from the fossil record, and from the reconstruction of plate tectonics. In 2010, for example, Maria Nilsson of the University of Munster and her colleagues published a detailed molecular phylogeny of all the major marsupial groups in the world (Nilsson et al. 2010). They based their analysis on retroposons, a type of mobile genetic element that sometimes is copied and inserted into a new location in an organism's DNA. After analyzing 53 retroposons, Nilsson and her colleagues concluded that all Australian marsupials form a clade, nested within a clade of South American species, that represents a single dispersal event from South America to Australia (**Figure 14.6**).

A molecular phylogeny can show only the relationships of species from which scientists can obtain DNA. A morphological phylogeny, on the other hand, can include fossil species as well (although it's typically based on fewer characters; see Chapter 4). The addition of fossil evidence complements the molecular evidence for the evolution of marsupials. A phylogeny of the major marsupial lineages known from fossils, based on morphological characters (Figure 14.6B), shows the same monophyly of Australian marsupials. It also reveals that marsupials lived in Antarctica when it was warmer, and that these extinct Antarctic marsupials were more closely related to living Australian marsupials than to South American ones. Finally, it shows that extinct North American marsupials belong to the deepest of the branches. This branching pattern parallels the order in which these continents separated from each other. North America split off first; next, South America separated from Australia and Antarctica; and lastly, Australia and Antarctica became separate landmasses.

These separate lines of evidence all support the same scenario for the evolution of marsupials (Springer et al. 2011). Marsupial-like mammals were living in China by 150 million years ago, the age of the oldest fossils yet found. By 120 million years ago, they had dispersed into North America, which at the time was linked to Asia. Many new lineages of marsupials evolved in North America over the next 55 million years.

From North America, some marsupials dispersed to Europe, even 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 (Beck et al. 2008). Another group of North American marsupials dispersed to South America around 70 million years ago.

A

C

Monodelphis
Didelphis
Metachirus

Rhyncholestes
Caenolestes

Dromiciops

Notoryctes

Phascogale
Dasyurus
Sminthopsis
Myrmecobius

Macrotis
Perameles
Isoodon

Tarsipes
Pseudocheirus

Trichosurus

Macropus
Potorous
Vombatus

Late Jurassic–Early Cretaceous
(150–120 million years ago)

North America
Europe
Africa
Asia
South America
Australia
Antarctica

Late Cretaceous–Paleogene
(70–55 million years ago)

Paleogene
(40–25 million years ago)

Pliocene
(3 million years ago)

B

Area cladogram

NORTH AMERICA
Ancient North American didelphoids

SOUTH AMERICA
South American didelphoids
South American microbiotheres

ANTARCTICA
Antarctic microbiotheres

AUSTRALIA
Australian marsupials
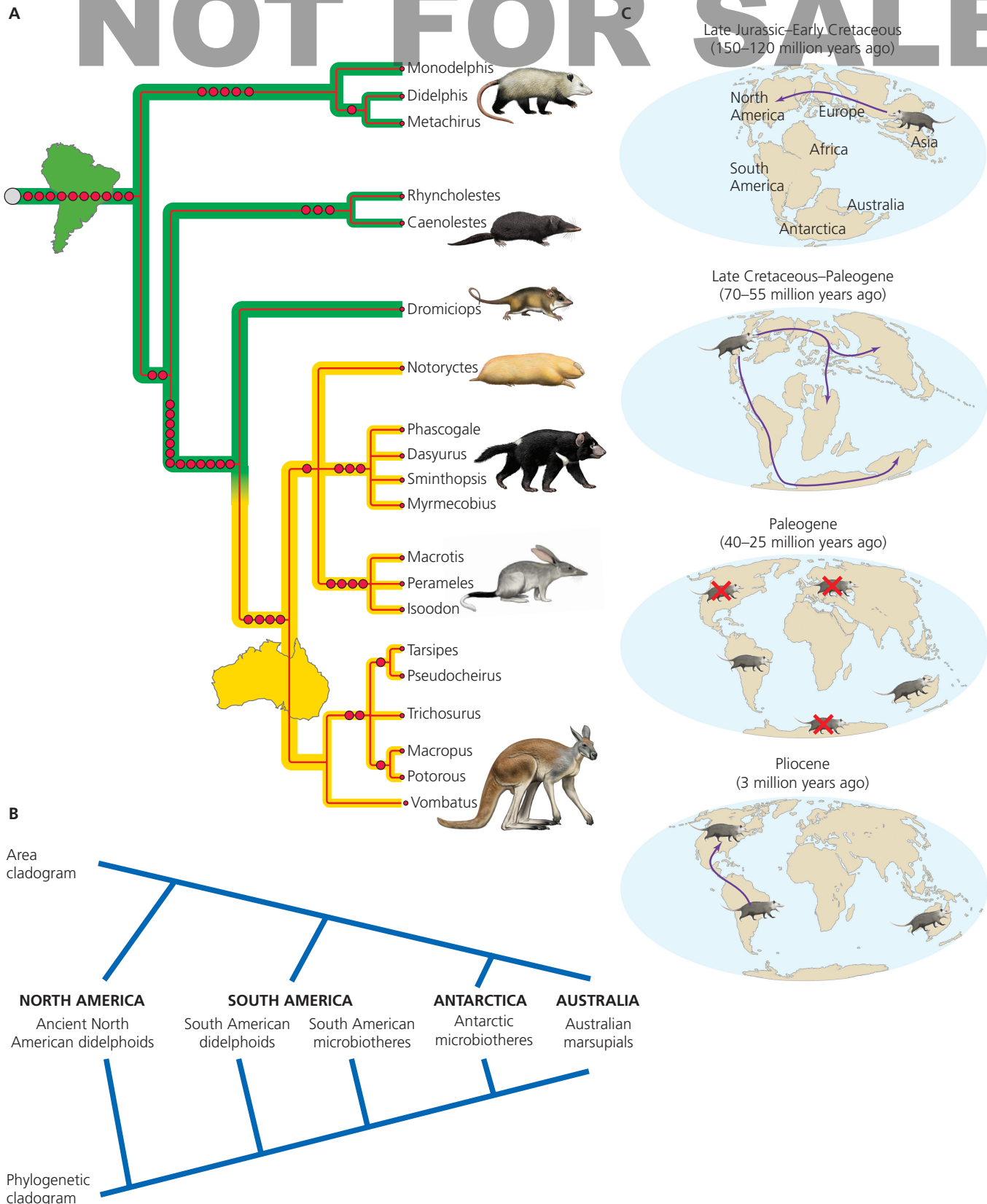
Phylogenetic cladogram

Figure 14.6 Marsupials evolved through a mix of vicariance and dispersal. A: Molecular phylogeny shows that Australian marsupials form a clade nested with South American marsupials. The only living North American marsupial, the Virginia opossum (*Didelphis*), is also nested within the South American clade. Dots denote retroposons uniquely shared by marsupial clades. (Adapted from Nilsson et al. 2010.) B: Separate lines of evidence also add insight into marsupial biogeography. A cladogram showing the ranges of marsupial lineages (known as an area cladogram) shows that marsupial phylogeny tracks the major separations of continents (top) and tracks a phylogenetic cladogram of known fossil lineages based on morphological characters (bottom). C: By combining this evidence, we can construct a scenario for the evolution of marsupials.

From South America, this branch of marsupials dispersed 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 (vicariance). 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.

Meanwhile, marsupials in South America diversified into a wide range of species, 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. Competition with placental mammals dispersing from North America may have been an important factor driving this extinction. However, there are still many different species of small and medium-sized marsupials living in South America today. One South American marsupial, the Virginia opossum, even expanded back into North America, where marsupials had disappeared millions of years before.

Australia, meanwhile, drifted in isolation for over 40 million years. The fossil record of Australia is currently too patchy for paleontologists to say whether there were any placental mammals in Australia during that time. Abundant Australian fossils date back to about 25 million years ago, when all of the therian mammals in Australia 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 colonizing the continent. These invaders diversified into many ecological niches, but there's no evidence that they displaced a single marsupial species that was already there (Christopher Norris, personal communication).

Key Concepts

- Biogeography is a highly interdisciplinary field that explores the roles of geography and history in explaining the distributions of species in space and time.

- Dispersal and vicariance explain distribution patterns of taxa. Dispersal occurs when a taxon crosses a preexisting barrier, like an ocean. Vicariance occurs when a barrier interrupts the preexisting range of the taxon, preventing gene flow between the now separated populations.

14.2 The Drivers of Macroevolution: Speciation and Extinction

To measure species diversity through time, scientists have adapted a method from population ecology. Population ecologists chart the growth of populations through time by a formula. They start with a population's current size, add births and immigrations, and subtract deaths and emigrations of individuals. In the formula shown here, N_1 stands for the current size of a population, and N_2 stands for the size of the population in the next time step.

$$N_1 + \text{births} + \text{immigrations} - \text{deaths} - \text{emigrations} = N_2$$

When scientists study macroevolution, they can adapt the formula, making species or higher clades their units of analysis instead of individual organisms. Likewise, they can substitute the originations and extinctions of species for the birth and death of individuals. The number of species in a region can also be altered through immigration and emigration. Here, D stands for the diversity—that is, the total number of species in a particular clade.

$$D_1 + \text{originations} + \text{immigrations} - \text{extinctions} - \text{emigrations} = D_2$$

In many cases, scientists study macroevolution on a global scale, rather than in one particular region. In these cases, we can eliminate the immigration and emigration terms from the equation:

$$D_1 \text{ (diversity)} + \text{originations} - \text{extinctions} = D_2 \text{ (new diversity)}$$

This simple equation brings into focus a fundamental idea about macroevolution: changes in diversity through time can be studied by looking at the interplay between origination and extinction. We can look at these processes in entire faunas (many different kinds of organisms in single ecosystems, regions, or at a worldwide scale). We can also look at them within a single clade, tracking its fluctuations in diversity through time.

We can illustrate this method with a hypothetical example, shown in **Figure 14.7**. A vertical bar represents the temporal range of fossils belonging to each species. The fossils were deposited in four consecutive geological stages marked here as A, B, C, and D. If we add up the fossils present at any point during stage A, we find a total of 24 species. During stage B, 10 new ones evolved, bringing the total to 34. But 6 species did not survive beyond B; the total in C is thus 36—only 2 species more than in B, despite the emergence of 8 new species. During D, another combination of originations and extinctions dropped the total to 30 species.

The total number of originations and extinctions in a given interval of time is known as **turnover**. In the example shown in Figure 14.7, a total of 20 turnovers occur in stage C (8 originations plus 12 extinctions). Turnover rates can tell us many important things about extinct clades. Paleontologists have found that some clades have especially high turnover rates, while others have low ones. Trilobites, for example, had very high turnover rates. Each trilobite species had only a brief duration in the fossil record, but the trilobite clade persisted because new species continued to arise at least as fast as earlier ones disappeared. Other groups, such as clams and snails, appear to have had relatively low turnover rates. Their species last much longer, and new species appear less frequently.

Turnover refers to the disappearance (extinction) of some species and their replacement by others (origination) in studies of macroevolution. The turnover rate is the number of species eliminated and replaced per unit of time.
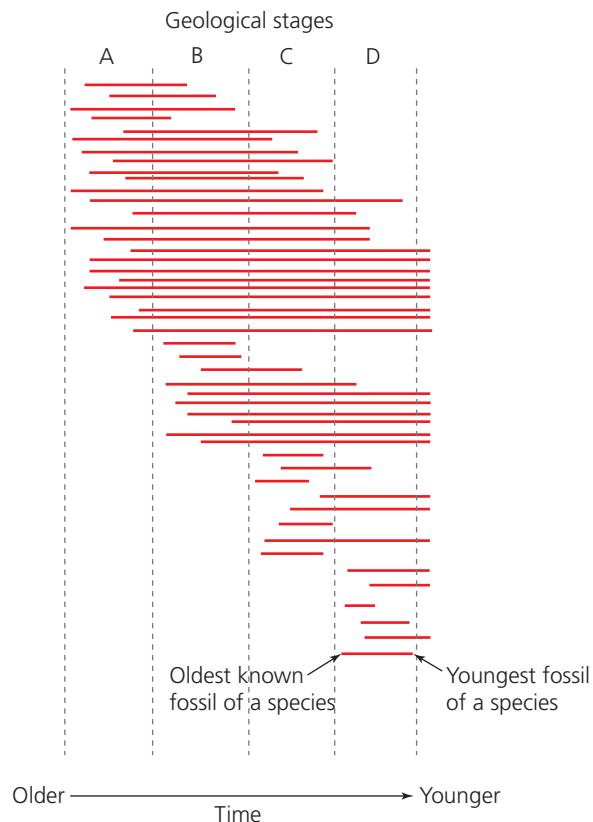

Figure 14.7 This hypothetical diagram shows how species are preserved in the fossil record. Paleontologists can calculate rates of processes such as origination and extinction from these kinds of data.

These shifts in diversity result from changes in both the rate at which new species evolve and the rate at which old species become extinct. We can represent the rate at which new species evolve, or originate, in a clade by the Greek letter α (alpha), and the rate at which species go extinct by Ω (omega). In Figure 14.7, the mean origination rate for the three stages B, C, and D is 8 new species per stage, while the mean extinction rate is 9 species per stage. Although our sample is not very large, we can see that 12 extinctions in stage C is more than usual, and that on average the extinction rate is slightly greater than the origination rate.

In the example shown in Figure 14.7, we measure the rate of origination and extinction in terms of species per stage. Radiometric dating of stages makes it possible to measure these rates by using years instead. If the stages shown in Figure 14.7 were each 6 million years long, for example, then α would be 1.3 species per million years, and Ω would be 1.5 species per million years.

The origination and extinction rates in a clade determine the total diversity at any given time—a value known as **standing diversity**. Over long periods of time, differences in α and Ω can lead to large changes in the diversity of a clade. If Ω becomes higher than α, the diversity of a clade will decline. But diversity can also decline if α drops. Likewise, either a drop in Ω or a rise in α will lead to an increase in diversity. Changes in both of these rates can lead to superficially similar patterns, but paleontologists can discriminate between these alternatives by carefully inspecting the fossil record.

Scientists first developed methods for estimating α and Ω by using fossils, but more recently, they have also developed methods for analyzing molecular phylogenies (Harvey et al. 1994; Pyron and Burbrink 2013). In these analyses, scientists use a molecular clock (see Chapter 9) to date the nodes. They then test models of α and Ω that produce patterns most closely resembling the actual phylogeny. These molecular methods are especially useful for measuring α and Ω in clades with a poor fossil record but a large number of living species. Scientists are also developing new methods to combine molecular and fossil data into a single macroevolutionary model.

Measuring origination and extinction rates can shed light on many striking patterns of biological diversity. As we noted earlier, for example, the tropics have higher levels of diversity than temperate regions. Scientists have proposed several hypotheses to explain this pattern (Mannion et al. 2014). Some scientists argue that high levels of tropical diversity are the result of high α. In other words, new species originate faster in the tropics than elsewhere. On the other hand, some scientists argue that a low Ω is the cause of tropical diversity. In other words, species are less likely to become extinct in the tropics than elsewhere. And still other researchers argue that both factors are involved—they view the tropics as both a nursery *and* a museum.

Standing diversity is the number of species (or other taxonomic unit) present in a particular area at a given time.

Key Concepts

- Scientists use the rates of origination and extinction of species documented in the fossil record to examine the history of life on Earth.

- Originations occur when the fossil record indicates a lineage split into two distinct clades. The clade may be a single species or a higher group.

- An extinction occurs when the last member of a clade dies. Trilobites, for example, were a clade containing many species; the entire trilobite clade became extinct 250 million years ago.

14.3 Charting Life's Rises and Falls

While charting the diversity of life over time can provide important insights into macroevolution, it poses two challenges. One challenge is the task of distinguishing species based on their fossils alone (see **Box 14.1** for a further discussion). Another challenge is that the fossil record is far from a complete picture of past biodiversity.

For example, biologists have described 61,000 living vertebrate species, but paleontologists have described only about 12,000 fossil vertebrate species from the past 540 million years. There must be many, many other fossil species we have yet to find (International Institute for Species Exploration 2010).

A pioneering paleobiologist, David Raup of the University of Chicago, took on these challenges by amassing a tremendous database of marine invertebrate fossils (Raup 1972). These animals had several advantages over other taxa: they make mineralized tissues such as shells and exoskeletons that fossilize well, and many species produced huge populations that left an abundant record from the Cambrian onward. In the 1960s, Raup started to build a database that by 1970 included 144,251 species with information about each species such as the geological age in which it lived. He then calculated changes in diversity from the Cambrian to the present, finding intriguing rises and falls. Ever since, other researchers have been building on that database and starting others, and applying new statistical methods to get a more accurate understanding of macroevolutionary patterns (Alroy 2008; Jablonski 2010).

In the late 1970s, for example, Jack Sepkoski of the University of Chicago built on Raup's work by comparing the changes in diversity of different taxonomic groups in the marine fossil record (Sepkoski 1981). Sepkoski found that the diversity of groups through time was not random. In fact, certain groups rose and fell together with other groups with remarkable consistency. He could explain more than 90 percent of the data by grouping taxa into three great "evolutionary faunas" that succeeded each other through time (**Figure 14.8**).

These three faunas are called the Cambrian, Paleozoic, and Modern faunas. (The names refer to when the faunas reached their peak diversity.) The Cambrian fauna arose at the beginning of the Paleozoic. It was dominated by trilobites, inarticulate brachiopods, and coil-shelled mollusks known as monoplacophorans. Following a quick start, this fauna went into decline. Today, only one group each of inarticulate brachiopods and monoplacophorans survive.

Figure 14.8 Jack Sepkoski identified three faunas in the fossil record since the Cambrian. The Cambrian fauna arose at the beginning of the Paleozoic and quickly declined. The Paleozoic fauna arose in the Ordovician. The so-called Modern fauna has its roots in the Cambrian but came to dominate the planet after the end of the Permian, 250 million years ago. (From Sepkoski 1981.)
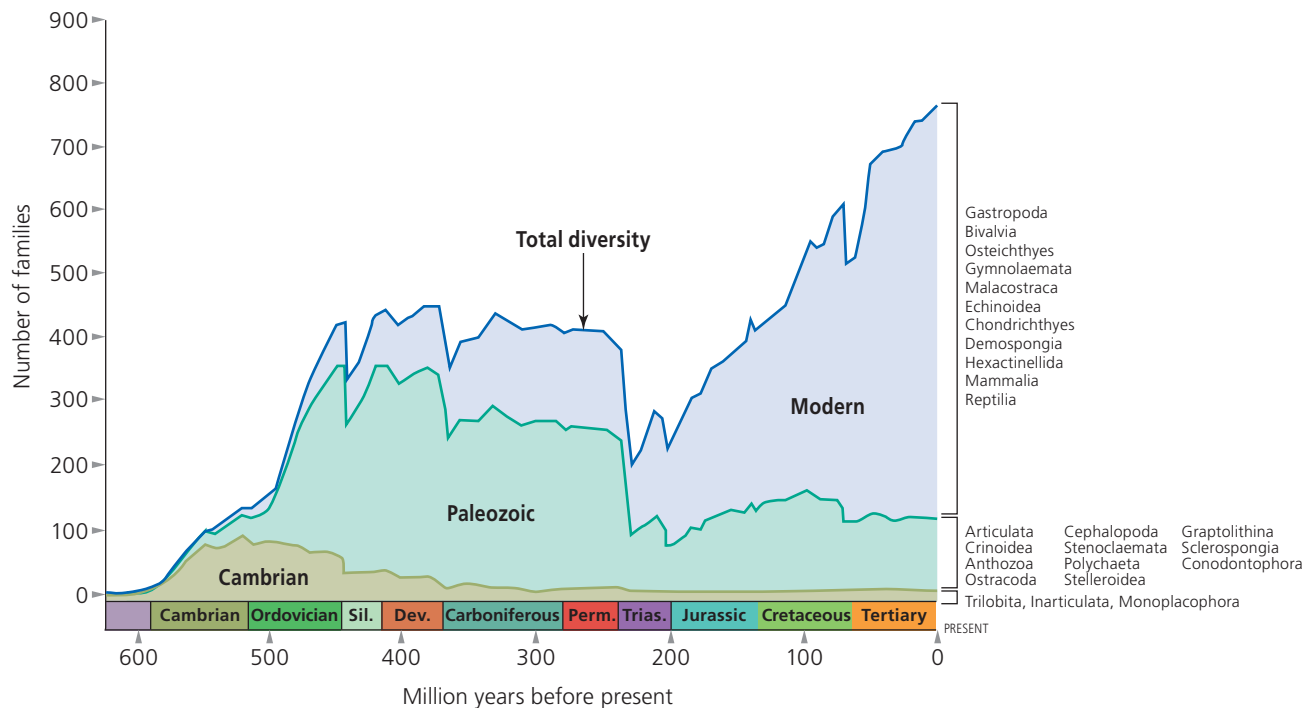
BOX 14.1

Punctuated Equilibria and the Species Concept in Paleontology

Throughout this chapter, we've been examining how the number of species has changed over the history of life. To do so, we must be able to count separate species in a reliable and accurate way. This is no easy task. As we saw in Chapter 13, biologists who study living species use several criteria to delineate their boundaries, such as breeding ability, morphological or genetic differences, geographical separation, and ecological differentiation. Paleontologists, on the other hand, can look only at the morphology of fossils to determine whether they belong to a previously described species or represent a new one.
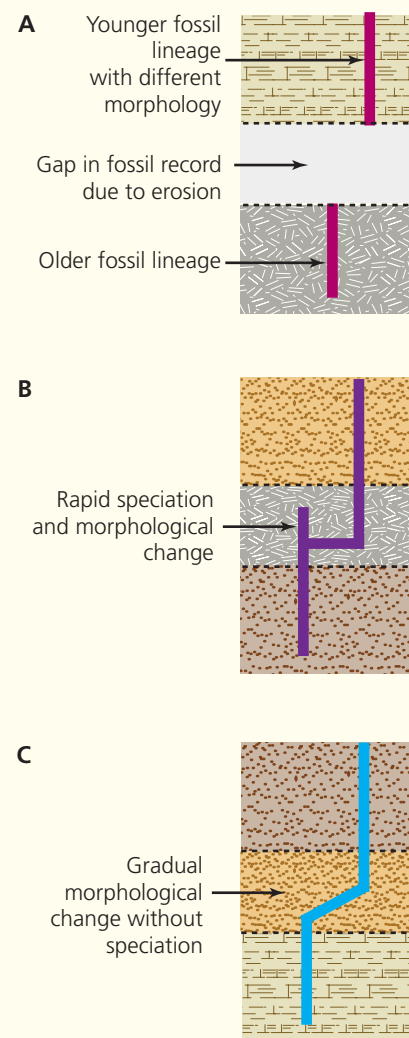
Using morphology to identify paleontological species creates some special challenges when we try to study the process of speciation in the fossil record. **Box Figure 14.1.1** illustrates what paleontologists often encounter when they excavate a series of fossils from a single lineage in a rock outcrop. The vertical axis represents the position of the fossils in the rock matrix. The fossils at the bottom are older, and the ones at the top are younger. The horizontal axis represents morphological variation—the shape of a gastropod's shell, for example. In Box Figure 14.1.1A, we first see a single "morph"—what we would accept as a paleontological species—at the base of the outcrop. As we move up in the section, we encounter some variability in this species, but nothing remarkable. Then we see a gap where there are no preserved fossils. Above the gap, there are more fossils. They are similar to the lower ones, but measurably different in the shape of their shell.

Do these younger fossils belong to the same species as the older ones? We can't tell. If the lower morph persisted into this upper level *alongside the new one*, we would have good reason to suspect that a speciation event had occurred, as shown in Box Figure 14.1.1B. Now two species existed where there had once been only one. Otherwise, we can choose between two possibilities. On the one hand, the old species might have split in two, but this split occurred when no fossils were being deposited. The original species went extinct during this time, while the new species survived. The other possibility is that during the undocumented time, the shape of the shell in the original species evolved into the new form. In the latter case, no speciation would have taken place. Instead, we would be dealing with a case of **anagenesis**.

Traditionally, paleontologists assumed that the imperfect fossil record hid smooth, gradual evolutionary change between species, as illustrated in **Box Figure 14.1.2** (Newell 1956). Because the fossils were separated by significant morphological differences, researchers assumed there must be gaps in the fossil record. If the fossil record were complete, it would show a gentle transformation from one form to the next.

In 1972 paleontologists Niles Eldredge and Stephen Jay Gould declared that this was an unjustified assumption (Eldredge and Gould 1972). They argued that most of the lineages documented in the fossil record experienced stasis; in other words, they exhibited little or no directional change for millions of years. The stasis was punctuated by relatively rapid change—enough to produce the

> **Anagenesis** refers to wholesale transformation of a lineage from one form to another. In macroevolutionary studies, anagenesis is considered to be an alternative to lineage splitting or speciation.

A Younger fossil lineage with different morphology

Gap in fossil record due to erosion

Older fossil lineage

B Rapid speciation and morphological change

C Gradual morphological change without speciation

Box Figure 14.1.1 Paleontologists often find fossils of a species that show relatively little change over time. Above a discontinuity, they find a new species with morphological differences, as shown in panel A. There are two possible explanations for this pattern: a new species may have branched off the old one, rapidly evolving morphological differences before entering its own stasis (B); or the old species underwent anagenesis, rapidly evolving a new morphology (C).

kind of differentiation seen between closely related species. This change was too fast to be preserved in the sparse fossil record, thus creating the appearance of a gap.

Eldredge and Gould dubbed this pattern **punctuated equilibria** (**Box Figure 14.1.3**). *Equilibria* referred to the stasis in lineages through a fossil sequence, which were punctuated by bursts of

> **Punctuated equilibria** is a model of evolution that proposes that most species undergo relatively little change for most of their geologic history. These periods of stasis are punctuated by brief periods of rapid morphological change, often associated with speciation.

change. Eldredge and Gould argued that these bursts were consistent with a principal model of speciation recognized by population biologists—the peripheral isolate model. Instead of the gradual divergence of a big population into two new lineages, the peripheral isolate model proposed that geographic isolation can cause fairly rapid evolution if a relatively small portion of the species becomes isolated on the fringes of the species' range.

If this mechanism of speciation occurred frequently, Eldredge and Gould argued, then we should expect abrupt morphological breaks in the fossil record. Few fossils will be evident from a species in the act of splitting.

In Chapter 8 we saw how evolutionary biologists have documented that natural selection can change allele frequencies in a matter of years or less. Such examples of rapid natural evolution are not in conflict with punctuated equilibria. When populations oscillate, as they did in Darwin's finches (Figure 8.5), the changes are viewed as "wobbles" in an otherwise stable lineage. But we saw in Chapter 10 how simple changes in the expression of developmental regulatory genes could generate spectacular and "sudden" changes in morphology, dramatic shifts in form that would definitely punctuate the history of a lineage.

As with any hypothesis in science, the punctuated equilibria model has been scrutinized (Pennell et al. 2014). For example, punctuated equilibria equates a substantial morphological shift—anagenesis—with speciation. Jeremy Jackson, a marine biologist, and Alan Cheetham, a paleontologist, tested an important assumption about this hypothesis with bryozoans: do the morphologies of

fossil and living bryozoans separate into species in a similar manner? The researchers compared morphological differences in fossil and living bryozoans against molecular and genetic assessments of difference in living forms. They found that morphology was a very good guide to the taxonomy of living bryozoans, as it was for fossil ones. Therefore, based on morphology, a fossil "species" is reasonably comparable to a living species (Jackson and Cheetham 1994). Jackson and Cheetham later extended their study to a variety of other marine invertebrates and microorganisms and found that the "punctuated" pattern clearly predominated. Paleobiologist Gene Hunt of the Smithsonian Institution found a similar pattern, in which stasis dominated the fossil record (Hunt 2006). Consequently, punctuated equilibria endures as an influential model of macroevolution.

Key Concepts

- In macroevolutionary studies, speciation events can be difficult to discern because changes in the morphologies of fossils are often the only clues available, and gaps in the fossil record may leave important transitions undocumented.

- Some of the controversy surrounding punctuated equilibria reflected the different timescales at which paleontologists and microevolutionary biologists operated. A "sudden" change in the fossil record might easily encompass 100,000 years, plenty of time for new species to arise from graded changes and "gradual" divergence in form.

Box Figure 14.1.2 Traditionally, paleontologists explained the pattern in the fossil record with gradual anagenesis, as in this diagram (adapted from Newell 1956). Hatched areas marked A–D are preserved sediment; white spaces are inferred gaps in the stratigraphic record.

A

B

Metrarabdotos
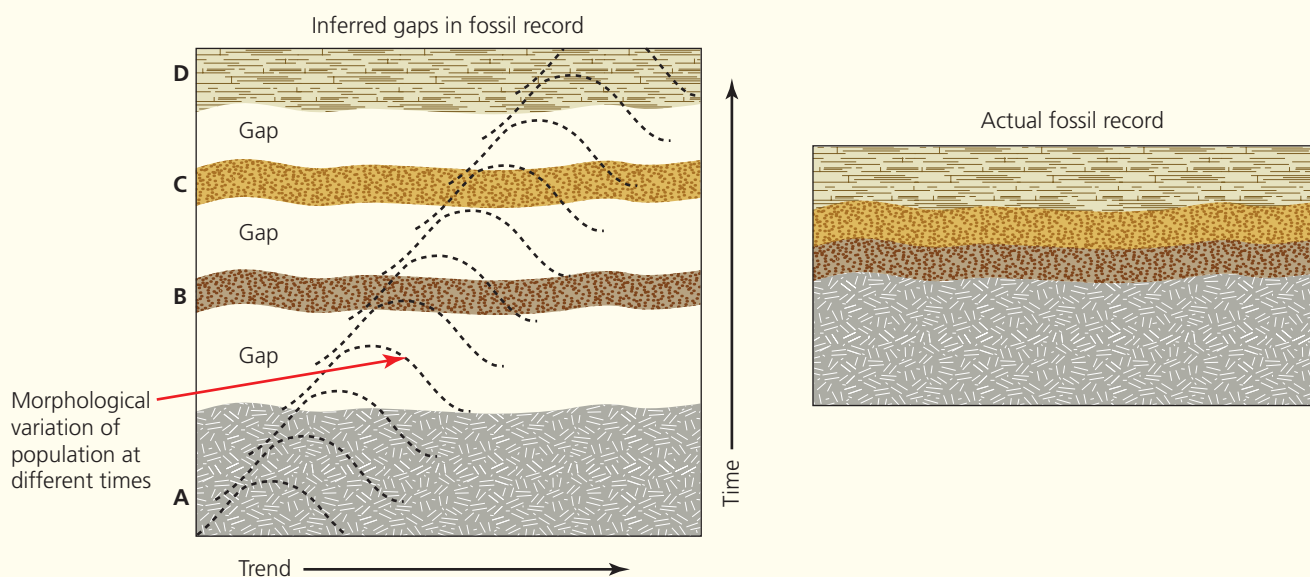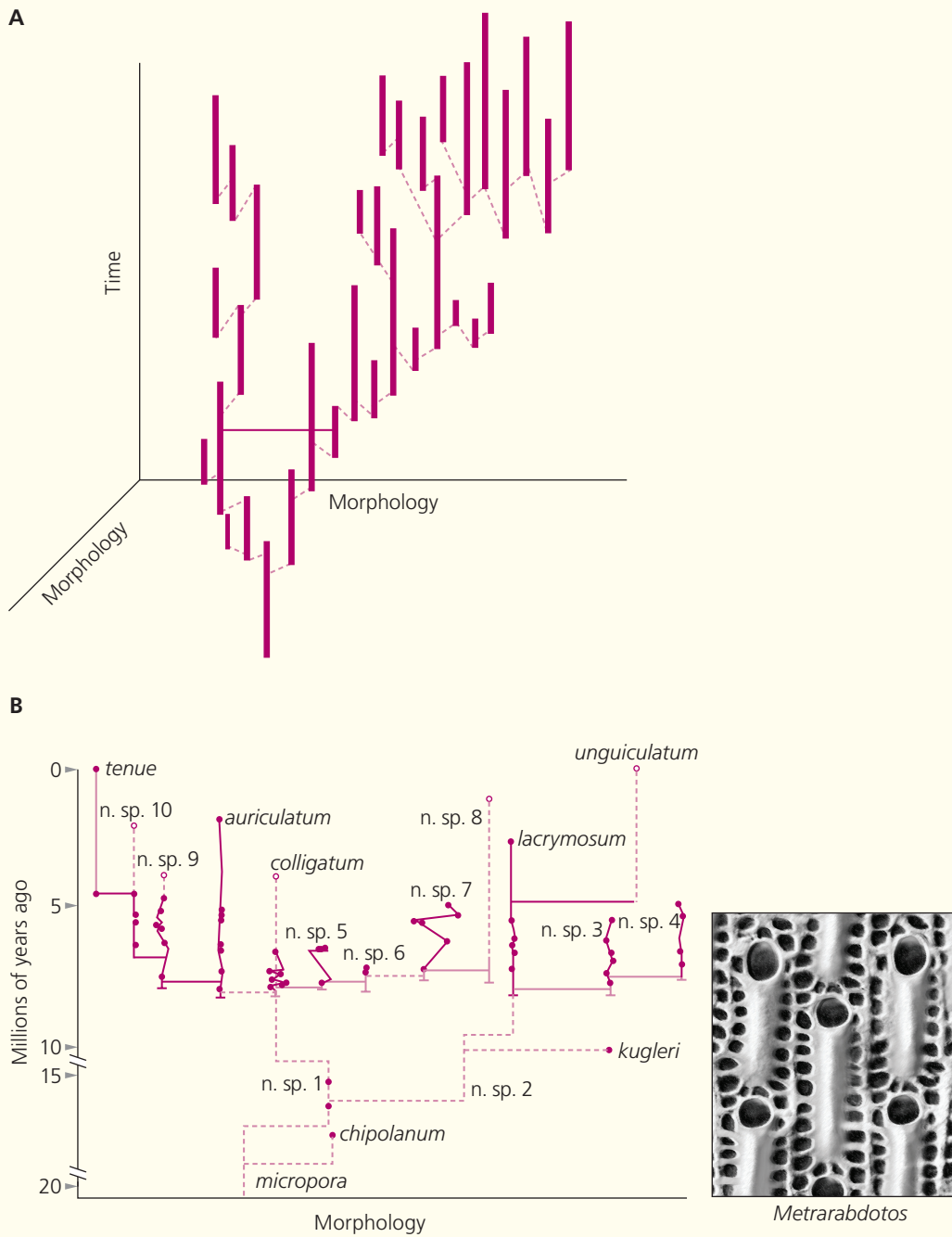
Box Figure 14.1.3 A: In 1972 Niles Eldredge and Stephen Jay Gould published an influential paper in which they argued that macroevolution was dominated by a pattern of punctuated equilibria. Species experienced long periods of stasis, punctuated by rapid morphological change during speciation. This is in contrast to the traditional model of slow, steady directional change in fossil lineages, which turns out to be surprisingly rare. (Adapted from Eldredge and Gould 1972.) B: Paleontologists have found a number of patterns in the fossil record that best fit the punctuated equilibria model. This diagram shows how a lineage of bryozoans (*Metrarabdotos*) evolved rapidly into new species, but changed little once those species were established. (Adapted from Benton 2003.)

By the Ordovician, Sepkoski found, the Cambrian fauna was overshadowed by the Paleozoic fauna, which was rich in various brachiopods, echinoderms, corals, crustaceans, ammonite mollusks, and many other groups. These groups thrived until the end of the Permian, 250 million years ago, when the biggest mass extinction in the fossil record wiped out up to 96 percent of marine species (we'll discuss this extinction in more detail later in this chapter). Most of these groups never recovered, and some major groups became extinct.

The Modern fauna has its roots in the Cambrian era, although its members were of relatively low diversity at the time. After the Cambrian, it climbed gradually in numbers. The Modern fauna, which has been dominant since the end-Permian extinction, consists mainly of gastropods (snails) and bivalves (clams).

14.4 The Drivers of Macroevolution: Changing Environments

When we see large-scale patterns of macroevolution such as Sepkoski's three faunas, we can test hypotheses to explain them. Scientists have found evidence for two types of factors involved in macroevolutionary change. Intrinsic factors, such as the physiology of clades, can play a role. Extrinsic factors in the environment can as well.

Sepkoski, for example, proposed that the transition between faunas may have been driven by their differences in origination (α) and extinction (Ω) rates. The invertebrates that dominated the Cambrian fauna (especially trilobites) had very high turnover rates, those of the Paleozoic fauna had moderate ones, and those of the Modern fauna (particularly clams and snails) had low ones. In other words, when it comes to animal evolution, slow and steady may win the race (Sepkoski 1981; see also Valentine 1989).

On the other hand, Shanan Peters, a paleontologist at the University of Wisconsin, has found possible physical factors involved in these changes: the geological context of Sepkoski's three faunas. He observed 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. The ecosystems built on these rocks may favor preservation of certain clades over others.

Over the past 540 million years, carbonate rocks have become rarer while silicoclastic rocks have become more common, possibly because of sediment delivered to the oceans by rivers. Peters proposed 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 (Peters 2008).

Another physical factor drives long-term changes in biodiversity: the climate. Earth is warmed by incoming radiation from the sun (**Figure 14.9**). Changes in the planet's orbit or angle to the sun can alter the amount of radiation it receives. Once this energy reaches Earth, it can be stored in the atmosphere or ocean, or it may be bounced back into space. The chemical composition of the atmosphere can change the amount of heat it traps. The concentration of heat-trapping gases, such as carbon dioxide and methane, is influenced by many factors, from the absorption of carbon dioxide by photosynthesizing plants and algae to the eruptions of carbon-dioxide-rich plumes from volcanoes.

Geologists can reconstruct the history of Earth's climates by looking at the chemistry of its rocks. Warm water has a higher concentration of the isotope oxygen-18 than cool water does, for example, and so rocks that form in warm water will lock in those isotopes as well.

Figure 14.9 Earth's climate is influenced by changes in incoming radiation from the sun and the chemical composition of the atmosphere. Large changes in the climate—both warming and cooling—can drive extinctions. The numbers by each arrow shows the watts per square meter being absorbed or released by the atmosphere and Earth.
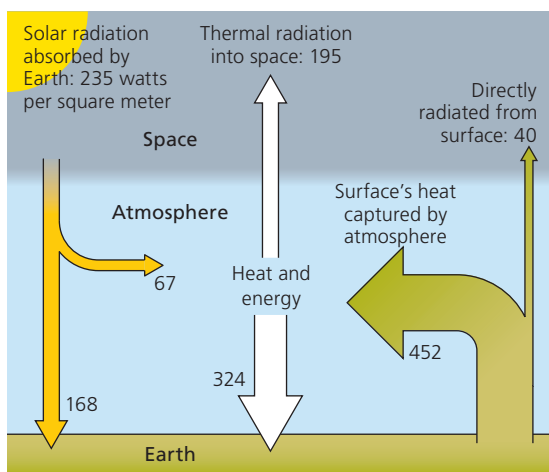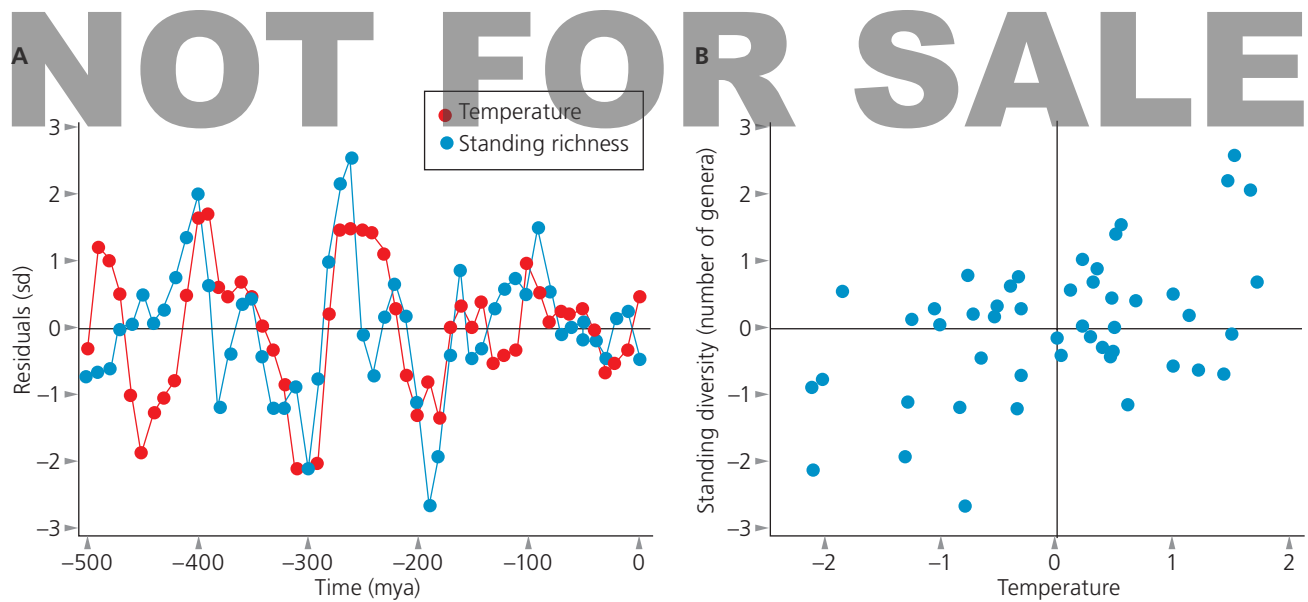
Figure 14.10 Taxonomic diversity (number of genera) is positively correlated with global mean ocean temperature. A: Over a span of 500 million years, the global mean temperature (red circles) fluctuated dramatically. Global levels of biodiversity also fluctuated (blue circles; both shown as deviations from their 500-mya average). B: Warmer periods had higher global levels of standing diversity than cooler periods. (Adapted from Mayhew et al. 2012.)

These records have demonstrated that Earth's climate has indeed fluctuated over the planet's history. One major source of this variation is the amount of carbon dioxide in the atmosphere. When certain types of volcanoes erupt more, they deliver more of these heat-trapping greenhouse gases to the atmosphere.

Peter Mayhew of the University of York examined how these changes in climate might affect the diversity of life. As we saw earlier, differences in climate have been proposed to explain the different levels of diversity found today in the tropics and in temperate zones. Mayhew and his colleagues looked to see if changes to the entire planet's climate could lead to changes in diversity. By carefully comparing the fossil record with the climate record, Mayhew and his colleagues did indeed find a correlation. After correcting for sampling biases in the fossil record, they found that periods with warmer ocean temperatures also had increased standing diversity of marine invertebrates (**Figure 14.10**; Mayhew et al. 2012).

Key Concept

- Because the fossil record is incomplete, examining macroevolutionary patterns over time is challenging. Statistical analyses can control for known biases and help scientists make and test predictions about the processes that shaped the observed patterns.

14.5 Adaptive Radiations: When α Eclipses Ω

The research we've examined so far looks at macroevolution at a global scale. Sepkoski and Raup, for example, studied marine fossils collected across the whole world. But even on a local scale, macroevolution can produce striking patterns that intrigue scientists.

Take, for example, the islands of Hawaii. As we discussed in Chapter 13, Hawaii is home to 37 species of swordtail crickets found nowhere else. Hawaii is also home to other remarkable clades, such as more than 50 species of honeycreeper birds. What's particularly striking about Hawaiian honeycreepers is that they have evolved dramatically different beaks and other morphological traits (**Figure 14.11**). Silversword plants also diversified into an equally impressive range of forms (**Figure 14.12**). Clades like
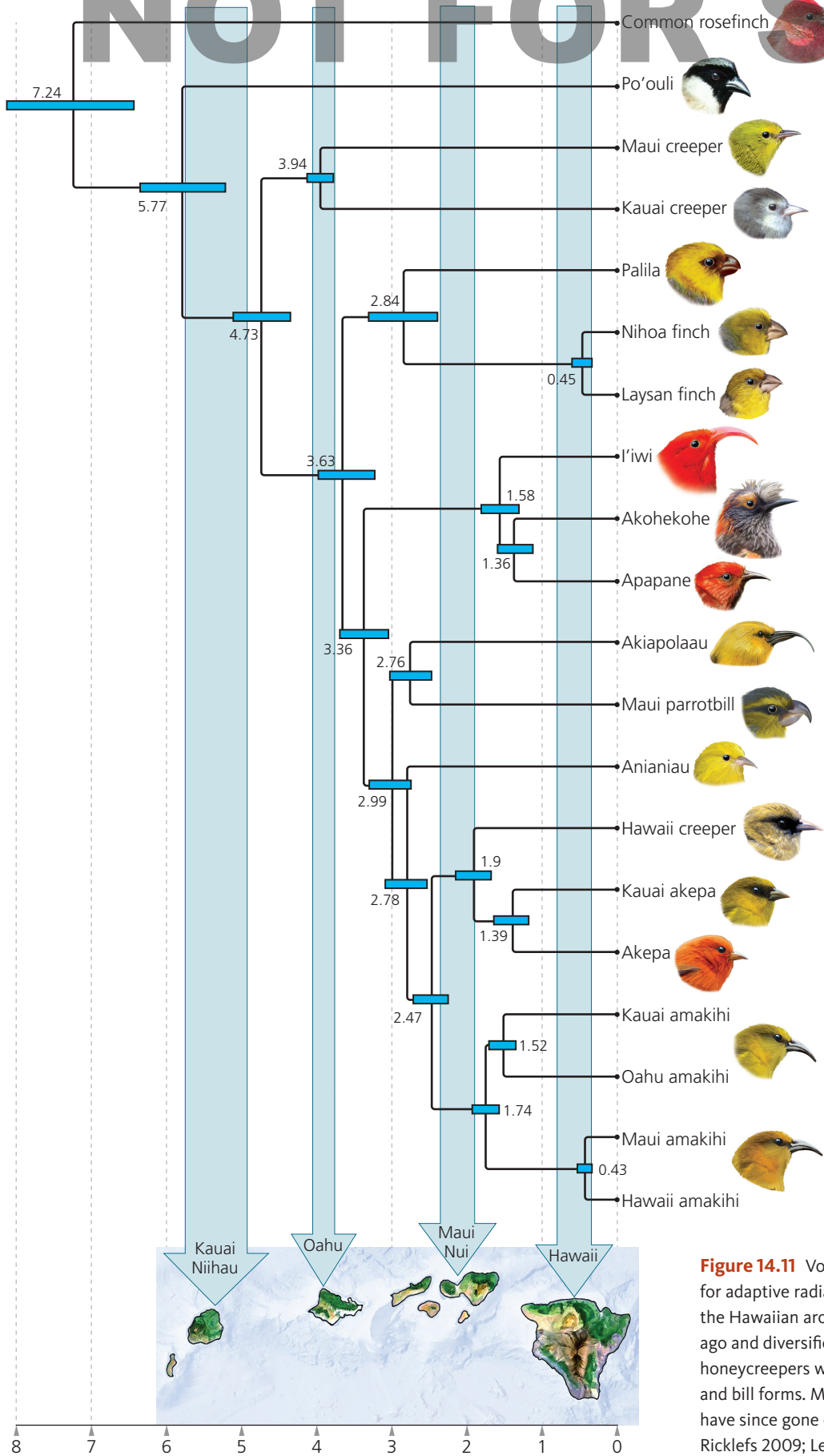
Figure 14.11 Volcanic islands provide backdrops for adaptive radiation. Ancestral finches colonized the Hawaiian archipelago roughly 5 million years ago and diversified into more than 50 species of honeycreepers with diverse colors, feeding habits, and bill forms. More than half of these species have since gone extinct. (Adapted from Losos and Ricklefs 2009; Lerner et al. 2011.)
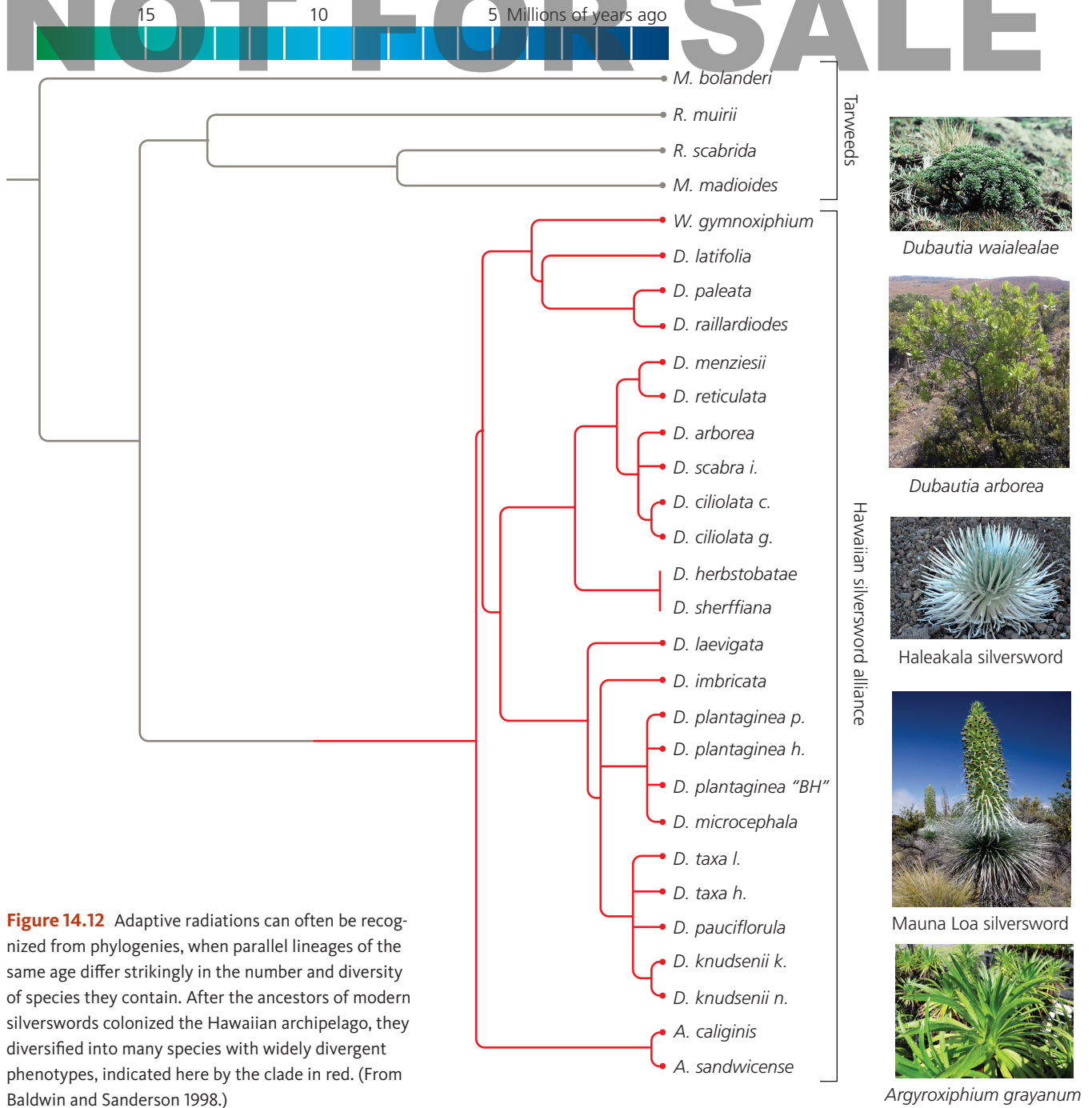
Figure 14.12 Adaptive radiations can often be recognized from phylogenies, when parallel lineages of the same age differ strikingly in the number and diversity of species they contain. After the ancestors of modern silverswords colonized the Hawaiian archipelago, they diversified into many species with widely divergent phenotypes, indicated here by the clade in red. (From Baldwin and Sanderson 1998.)

Dubautia waialealae

Dubautia arborea

Haleakala silversword

Mauna Loa silversword

Argyroxiphium grayanum

these, which have rapidly diversified by adapting to a wide range of resource zones, are known as **adaptive radiations** (Losos 2010).

Islands are not the only places where adaptive radiations take place. The Great Lakes of East Africa are geologically very young, in many cases having formed in just the past few hundred thousand years (Sturmbauer et al. 2001). Once the lakes formed, cichlid fishes moved into them from nearby rivers. The fishes then diversified explosively into hundreds of new species. Along the way, the cichlids adapted to making a living in an astounding range of ways—from crushing mollusks to scraping algae to eating the scales off other cichlids (Kocher 2004; Salzburger et al. 2005).

During adaptive radiations, new lineages expand to occupy new ecological roles. As a result, adaptive radiations produce some of the most striking examples of evolutionary convergence. For example, when marsupials diversified in Australia, they converged on body forms represented on other continents by placental mammals (see

Adaptive radiations are evolutionary lineages that have undergone exceptionally rapid diversification into a variety of lifestyles or ecological niches.

Lake Tanganyika species	Lake Malawi species
Julidochromis ornatus	*Melanochromis auratus*
Tropheus brichardi	*Pseudotropheus microstoma*
Bathybates ferox	*Ramphochromis longiceps*
Cyphotilapia frontosa	*Cyrtocara moorei*
Lobochilotes labiatus	*Placidochromis milomo*

Figure 14.13 Adaptive radiations sometimes lead to impressive examples of convergent evolution. Cichlid fish diversified independently within adjacent African Great Lakes, and these simultaneous radiations resulted in striking parallels in feeding ecology and morphology.

Figure 10.27). The African Great Lakes cichlids also experienced convergent evolution as lineages adapted to the same lifestyles and habitats in different lakes (**Figure 14.13**).

Adaptive radiations may occur when clades evolve to occupy ecological niches in the absence of competition. These opportunities can arise with the emergence of a new island or lake. But they can arise in other ways as well. When extinctions remove certain species from an ecological resource zone, other lineages can evolve that take their place. Such appears to be the case for mammals. When large dinosaurs became extinct at the end of the Cretaceous, large mammals rapidly evolved and diversified (Smith et al. 2010).

In other cases, clades may radiate because new adaptations, known as key innovations, evolve that allow them to occupy habitats or adaptive zones that were simply off limits to earlier clades (**Table 14.1**). That seems to be what happened in the most diverse clade of animals on Earth, the insects. Insects first evolved about 400 million years ago, and today a million species of insects have been named. Probably millions more have yet to be described. Their closest relatives are a group called the entognathans, which includes springtails. The entognathans comprise only 10,600 species. And although entognathans generally look very similar to one another, insects have diversified impressively, from carnivorous dragonflies to ants that tend mushroom gardens to wasps that inject their eggs into living hosts.

Unlike the entognathans, the insects evolved wings that allowed them to occupy ecological roles unavailable to flightless invertebrates. Wings permitted insects to occupy new adaptive zones, and they also permitted them to colonize new habitats (Grimaldi and Engel 2005; Mayhew 2007; Nicholson et al. 2014). Other potential factors in the success of insects may include the evolution of herbivory. The ability to eat plants evolved several times within insects, and as we'll see in the next chapter, the plant-eating lineages tended to accumulate more species than did closely related lineages of insects that didn't eat plants.

TABLE 14.1 Examples of Adaptive Radiation, and the Circumstances Thought to Have Generated Ecological Opportunity in Each Case

TABLE 14.1 Adaptive radiations have occurred throughout history, mostly as the result of resources that were either completely new or newly available.

Taxa/Clade	Mechanism	Opportunity
Cambrian radiation of animals	Environmental change; key innovations (genetic toolkit, body segments, skeletal structures)	Increased O_2 availability; increased developmental capacity to diversify in form; colonization of new lifestyles (e.g., predators), habitats (mobile)
Devonian radiation of plants	Key innovations (seeds, vascular tissue)	Colonization of terrestrial environments
Cretaceous radiation of angiosperms	Key innovation (flowers)	Initiation of mutualistic coevolution with insects
Devonian radiation of insects	Key innovation (wings)	Colonization of the air
Cenozoic radiation of mammals	Extinction of dinosaurs, large reptiles	Undercontested resources/niches
Radiation of Darwin's finches	Colonization of Galápagos archipelago	Undercontested resources/niches
Radiation of silver-swords, fruit flies, honeycreepers	Colonization of Hawaiian archipelago	Undercontested resources/niches
Radiation of cichlids	Colonization of African Great Lakes	Undercontested resources/niches

Key Concepts

- Most adaptive radiations have a common theme: the absence of established competitors for the resources within an environment. Undercontested resources permitted ancestral populations to flourish and adapt to increasingly specialized and localized subsets of those available resources and/or habitats, leading to diversification and speciation.

- Sometimes intrinsic properties of a lineage create ecological opportunity. Key innovations can transform how organisms interact with their environments in ways that take them into new and undercontested habitats or permit them to exploit novel ways of life. These opportunities can trigger explosive subsequent diversification and adaptive radiation.

14.6 The Cambrian Explosion: Macroevolution at the Dawn of the Animal Kingdom

As spectacular as the adaptive radiation of insects may have been, it was, in some respects, a modest event. Every species of insect retains the same body plan. But the insect radiation was preceded by a far more dramatic one that occurred about 540 million years ago. It gave rise to many of the major groups of animals found on Earth today, each with its own distinctive body plan. Known as the Cambrian Explosion, it stands as one of the most important macroevolutionary events in the history of life (Erwin and Valentine 2013).

The first signs of the Cambrian Explosion emerged in the nineteenth century, as paleontologists began to organize the fossil record. They found that remains of animals reached back to the Cambrian period. At their earliest appearance, animals were