Speciation often occurs in patterns.

Paleontologists have long noticed repeating patterns in the history of life, reflected in the fossil record. Among these patterns, two stand out from the rest. In evolutionary gradualism, discussed in Section 2 of the chapter Principles of Evolution, evolutionary changes are thought to occur over long periods of time. For many years, advocates of evolution adhered to this idea.

In the second of the two patterns, bursts of evolutionary activity are followed by long periods of stability. This pattern is described by the theory of **punctuated equilibrium**, which states that episodes of speciation occur suddenly in geologic time and are followed by long periods of little evolutionary change, or stasis. Paleontologist Niles Eldredge, a curator at The American Museum of Natural History in New York, and evolutionary biologist Stephen Jay Gould originally proposed the theory of punctuated equilbrium in 1972. Both men were graduate students at Columbia University, studying fossils of four closely related species of trilobite. The fossils showed evidence of the sudden appearance of a new form of eye. This new trilobite eye appears to be linked to an increased ability to roll into a protective ball, allowing for better defense against predators.

The theory of punctuated equilibrium was written as a revision of Darwin's idea that new species arise through gradual transformations of ancestral species. It must be noted that in the sixth edition of his book *On the Origin of Species*, Darwin wrote that "the periods, during which species have undergone modification, though long as measured by years, have probably been short in comparison with the periods during which they retained the same form."

GEOLOGY

Refer back to Section 1 of the chapter **Principles of Evolution** to review James Hutton's theory that led to the concept of evolutionary gradualism.

FIGURE 6.6 Evolutionary Gradualism and Punctuated Equilibrium

The concept that species evolve slowly, over long periods of time, is known as evolutionary gradualism.





vears, followed by periods of rapid speciation

Modern studies show us that in stable ecosystems, most species are well adapted and generally resistant to change, unless some outside force causes disruption. In the case of punctuated equilibrium, this is believed to occur because a portion of a population becomes isolated and undergoes a speciation event. This isolation may be due to some sort of catastrophe, after which those organisms able to evolve quickly are more likely to survive. Isolation may also occur as a result of long-term environmental changes, like the formation of mountains or deserts, or due to a mutation that gives the organism a significant survival advantage over competitors.

When an ecosystem is greatly damaged, such as after the 1980 volcanic eruption of Mt. Saint Helens, in Washington state, other organisms will rapidly move into the area to fill empty niches. Although rapid evolutionary bursts can be compared in some ways to what is seen when such modern ecosystems are seriously disturbed, there is a distinct difference between the two. Rather than existing species moving in to fill vacancies in a changed ecosystem, in punctuated equilibrium, new speciation occurs suddenly following a long



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This model of *Leptictidium* was made based on the bone structures found in fossil specimens.

interval of stasis. Both evolutionary gradualism and punctuated equilibrium are viable scientific theories, and both are supported by evidence found in the fossil record. Although scientists still debate which of these two ideas best accounts for observed patterns of evolutionary change, most accept that it is likely that evolution occurs by a combination of these two major theories.

The process involving the diversification of one ancestral species into many descendent species is referred to as **adaptive radiation**. These descendent species are usually adapted to a wide range of environments. One example of adaptive radiation

> is the variation found in Galápagos finches, which were discussed in the chapter Principles of Evolution. Another rather dramatic example is seen in the radiation of mammals following the mass extinction at the end of the Cretaceous period about 65 million years ago.

> According to the fossils that have been found thus far, the earliest mammals were tiny, mostly nocturnal, and probably insect eaters, such as the shrew-like *Leptictidium*, seen in **FIGURE 6.7**, allowing them to coexist with the dinosaurs for about 150 million years.

FIGURE 6.8 The K-T Boundary

The K-T boundary layer is marked clearly in rock layers in many places around the world. It is linked to the collision of an asteroid with Earth around 65 million years ago. The layer contains high concentrations of the element Iridium. Iridium is verv rare on Earth, but is found in much greater abundance in objects from space.

K-T BOUNDARY



The extinction of the dinosaurs about 65 million years ago left environments full of open niches for other types of animals. In the first 10 million years of the Tertiary period following the mass extinction event, more than 4000 mammal species had evolved, including the ancestors of modern whales, bats, rodents, and primates. Evidence of this mass extinction, known as the Cretaceous-Tertiary (K-T) boundary, can be seen in FIGURE 6.8.

The fossil record indicates that there have been at least five mass extinctions in the past 600 million years, where large percentages of global populations were decimated. Studying these extinctions reveals that following each was a period of rapid evolutionary changes and the appearance of new species.

Synthesize The adaptive radiation of mammals followed the extinction of the dinosaurs. How do these events support the theory of punctuated equilibrium?

11.6 **Formative Assessment**

REVIEWING O MAIN IDEAS

- 1. Explain what it means to say that natural selection is not random.
- 2. How does **coevolution** shape two species over time?
- 3. How can mass extinctions lead to the sudden appearance of new species?
- 4. What pattern is described by the theory of **punctuated equilibrium**?

CRITICAL THINKING

- 5. Synthesize Defensive chemicals are usually found in unripe fruit, but not in ripe fruit. In terms of coevolution, why might this be?
- 6. Infer Analogous structures are often examples of **convergent evolution**. What types of structures would likely be examples of **divergent evolution**?

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CONNECT TO **HUMAN BIOLOGY**

- 7. Through mutation, HIV can
- accumulate resistance to drugs developed for treatment. Describe the relationship between HIV and the humans who develop these drugs in terms of an evolutionary arms race.