14.10 The tempo of speciation can appear steady or jumpy

Although biologists continue to gather examples of evolution in progress, much of the evidence of evolution comes from the fossil record, the chronicle of extinct organisms engraved in layers of rock over millions of years of geologic time. Let's take a look at two models that have proved useful in interpreting the evolutionary patterns suggested by the fossil record.

Figure 14.10A illustrates the evolution of two lineages of hypothetical butterflies by what has been called the **gradualism model**. This model fits Darwin's view of the origin of species: Differences gradually evolve in populations as they become adapted to their local environments; and new species (represented by the two butterflies at the top) evolve gradually from the ancestral population. According to the gradualism model, big changes (speciations) occur by the steady accumulation of many small changes.

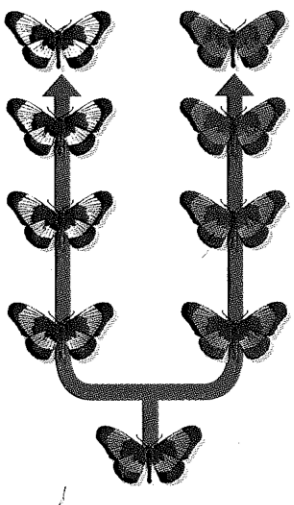

Figure 14.10A Gradualism model

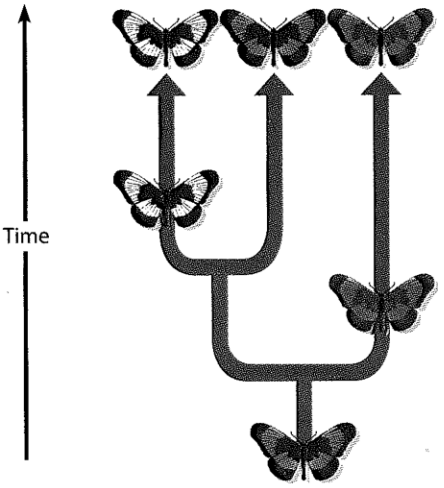

Figure 14.10B Punctuated equilibrium model

Many evolutionary biologists since Darwin's time, and even Darwin himself, have been struck by how few sequences of fossils have ever been found that clearly show a gradual, steady accumulation of small changes in evolutionary lineages. Instead, most fossil species appear suddenly in a layer of rock and persist essentially unchanged through several layers (strata) until disappearing from the record of the rocks as suddenly as they appeared. Paleontologists Niles Eldredge and Stephen Jay Gould coined the term **punctuated equilibrium** to describe these abrupt episodes of speciation punctuating long periods of little change, or equilibrium. Illustrated in Figure 14.10B, this model suggests that the evolution of our hypothetical butterflies actually occurs in spurts. Notice that, in contrast to the gradualism model, Figure 14.10B shows no transitional stages in the lineages. The butterflies look the same at the bottom and top of each lineage; the species change little, if at all, once they appear.

The fossil record suggests that successful species last for a few million years, on average. Suppose that a particular species survived for 5 million years, but that most of the changes in its body features occurred during the first 50,000 years of its existence, just 1% of the overall history of the species. Because time periods this short often cannot be distinguished in fossil strata, the species would seem to have appeared abruptly and continued, apparently unchanged, in rocks spanning millions of years before disappearing. Even though the emergence of this species actually took thousands of years, the overall history of the lineage as depicted in the fossil record may seem to fit the punctuated equilibrium model.

The periods of equilibrium in the fossil record may also be explained in a manner consistent with the gradualism model. All species continue to adapt after they come into existence, but often in ways that cannot be detected from fossils. By necessity, paleontologists base evolutionary hypotheses almost entirely on external anatomy and skeletons. During periods of apparent equilibrium, changes in behavior, internal anatomy, and physiology may go undetected.

Is it likely that most species evolve abruptly and then remain essentially unchanged for most of their existence? Rapid speciation certainly occurs in some cases. As we saw earlier, abrupt speciation can occur by polyploidy in plants and even in a few animals. It appears that genetic drift and natural selection can significantly alter the gene pool of a small population isolated in a challenging new environment in a few hundred to a few thousand generations. Also, mutation of just a few of the genes that regulate embryonic development may produce radically new body features, a topic we will explore in Module 14.12. Debates about the tempo of evolution continue to catalyze research and ultimately lead to a better understanding of the process.

Speciation may begin with small differences as one species gives rise to another similar species. However, as species diverge and speciate again and again, these differences accumulate and become more pronounced. Thus, speciation constitutes the beginning of macroevolutionary change. The more dramatic transformations associated with macroevolution are the topics we consider in the final modules of this chapter.

? How does the punctuated equilibrium model account for the relative rarity of transitional fossils linking newer species to older ones?

■ If speciation takes place in a relatively short time compared to the overall time the species exists, the transition of one species to another may be difficult to find in the fossil record.