OVERVIEW

Punctuated Equilibrium

Darwin survives
as the debate evolves

In 1972 two paleontologists, Niles Eldredge of the American Museum of Natural History and Stephen Jay Gould of Harvard University, startled—and in some cases dismayed—biologists by suggesting that the view of evolution most of them held was an "insufficient picture." Eldredge and Gould maintained that life was no stately unfolding of gradually changing forms that slowly divided to create new species. Rather, they believed, species formed relatively quickly as a result of rapid bursts of evolutionary change. Eldredge and Gould thought their colleagues were wrong to blame the rarity of intermediate fossil sequences on gaps in the fossil record. Instead they proposed that such sequences were rare because evolution did not happen that way. Eldredge and Gould considered it more likely that

new species evolve within a few thousand years, the mere blink of an eye in geologic time. Once a species has evolved, they argued, it enters a period of stasis, remaining unchanged for possibly millions of years. The two scientists called their theory punctuated equilibrium.

Eldredge and Gould did more than offer a new picture of evolution's progress. They also suggested that Darwin's theory of natural selection acting on individuals was inadequate, because it predicted gradual evolution of species in response to environmental change rather than a "punctuated" pattern. In order to reconcile punctuated equilibrium with the long-term trends seen in fossil lineages—such as the progression from smaller to larger species of mammals—Eldredge and Gould therefore proposed a variant of Darwin's theory. They suggested that natural selection not only acts on the individual level but must also be acting at the species level, an idea since termed species selection. According to this idea, lineages thrive if they either resist extinction or produce frequent daughter species. Gould even wrote that the "synthetic theory"—Darwin's theory of natural selection combined with genetics—was "effectively dead" as an explanation for long-term evolutionary trends.

Not surprisingly, these ideas attracted attention. Popular accounts fostered the impression that Darwin's theory of evolution was wrong. Creationists gleefully played up the argument in their effort to reshape biology teaching, despite Eldredge and Gould's protests that their theory was not meant to question the basic tenets of evolution.

How has punctuated equilibrium fared since it was first proposed almost 20 years ago? Many biologists say Eldredge and Gould attacked a straw theory: evolution has never been viewed as exclusively slow and gradual, they argue, and natural selection is quite able to account for the formation of species over thousands of years, as required by punctuated equilibrium. Ernst Mayr of Harvard University makes the point by quoting Darwin, who wrote in later editions of *On the Origin of Species* that "the periods during which species have been undergoing modification... have probably been short in comparison with the periods during which these same species remained without undergoing any change."

Mayr, who is often regarded as the dean of evolutionary biology, proposed in 1954 that "genetic revolu-

tions" in small, isolated populations may give rise to new species, an idea that Eldredge and Gould have acknowledged as inspirational. Mayr says that Eldredge and Gould have sometimes made "outrageous claims," but he believes they were correct to draw attention to stasis in fossil lineages. Mayr theorizes that such periods—some of which might last for tens of millions of years—are caused by genetic and developmental constraints that limit change.

Jeffrey S. Levinton of the State University of New York at Stony Brook is one of the strongest critics of punctuated equilibrium. He maintains there are "literally scores" of good examples of gradual change. He says Eldredge and Gould remind him of a Scandinavian aphorism: "People come crashing through open doors." How, for example, can the theory be tested when the formation of species cannot be clearly recognized in the fossil record? Levinton concludes that "the totality of the evidence makes it a theory not worth following up."

Antoni Hoffman of the Institute of Paleobiology in Warsaw, who has written a book aimed at refuting punctuated equilibrium, accuses proponents of the theory of creating a moving target. According to Hoffman's analysis, some versions of the theory claim merely that evolution varies in speed—which is undisputed. Later versions claim that gradual change is nonexistent or negligible; that, Hoffman maintains, is "blatantly false."

In 1987 Peter R. Sheldon, then at Trinity College in Dublin, seemed to score a direct hit against punctuated equilibrium when he reported finding that eight types of trilobite had each evolved gradually over a three-million-year interval during the Ordovician period, more than 440 million years ago. The finding prompted John Maynard Smith of the University of Sussex to comment that "we can forget about new paradigms and the death of neodarwinism." But the arguments persist, and each side continues to collect evidence. For example, Adrian M. Lister of the University of Cambridge reported in *Nature* recently that red deer on the island of Jersey underwent a sixfold reduction in their body weight in less than 6,000 years, suggesting that rapid evolution can indeed occur under some conditions.

Gould thinks Sheldon's interpretation of the trilobite record is weak, yet he maintains that paleontologists can discern the formation of new species in the fossil record through comparisons with living species. He admits that the evidence is not yet in and suggests that the technical difficulty of finding adequate data, in the form of well-preserved fossils from undisturbed sedimentary beds, has made for slow progress. While conceding that rapid change is not universal, Gould declares that he and Eldredge will be proved right if rapid species formation and stasis do turn out to dominate in the fossil record.

Where does that leave species selection? Most evolutionists seem to agree with Hoffman that it cannot explain features of individuals, although it might in principle explain some of the long-term trends in evolution. Yet there are no proven examples, and the idea may be, as Hoffman puts it, "an explanation in search of phenomena to explain." Montgomery W. Slatkin of the University of California at Berkeley argues that even if punctuated equilibrium does turn out to be common in evolution, it may nonetheless be driven by natural selection acting on individuals.

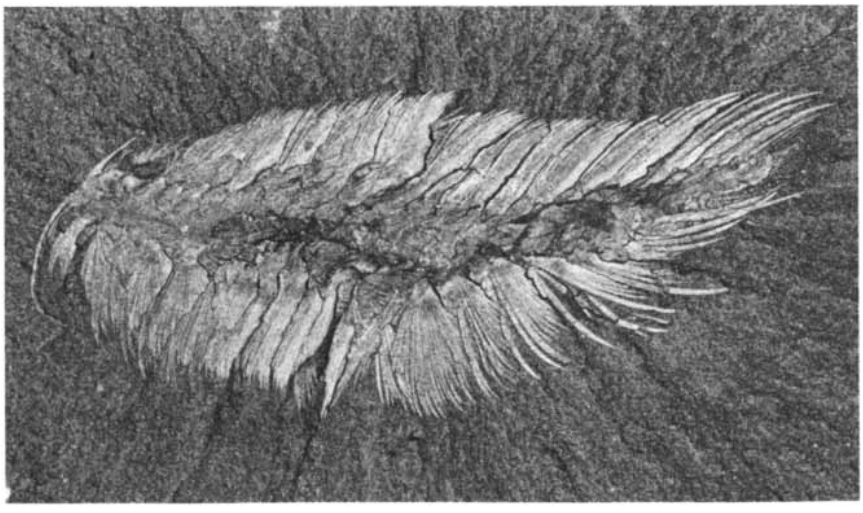
Species selection has even been criticized by a scientist whom Gould lionizes in his latest book, *Wonderful Life*. Gould recounts the story of the Burgess Shale in British Columbia, which contains the remains of bizarre soft-bodied animals that appeared on the earth some 530 million years ago, soon after the first emergence of multicellular creatures at the start of the Cambrian period. Work in recent decades has shown that not only are the Burgess fossils surprisingly complex, but few of them fit into known taxonomic classes.

One of the heroes of Gould's tale is Simon Conway Morris of the University of Cambridge, who painstakingly reconstructed some of the specimens. In a recent article in *Science*, Conway Morris writes that he sees no need for special evolutionary mechanisms (such as species selection) to explain the stunning diversity of the Burgess Shale. He adds that "there is no reason to think that any species did not arise by natural selection."

Gould responds that he finds it hard to imagine natural selection plays no part in the formation of species, but he emphasizes the role of chance in creating the genetic rearrangements that may generate them. Indeed, the importance of chance is the main lesson Gould draws from the Burgess Shale fossils. He maintains it would have been impossible for any biologist to predict which of the myriad Burgess Shale animals would give rise to later groups: he sees the survival of species as a lottery controlled by historical contingency.

On that point, Gould and his critics agree for once. The implications of a starring role for Lady Luck are profound. Were evolution's drama to be "replayed," the earth's fauna and flora would be radically different, and the human species—that "improbable and fragile entity"—would presumably not exist. —*Tim Beardsley*

Burgess Shale fossils are unlike any others, confounding efforts to classify them



CANADIA SPINOSA is one of the strange animals whose remains were found in the Burgess Shale. Stephen Jay Gould thinks the few early types that survived and gave rise to later groups were simply lucky.