Did Darwin Get It All Right?

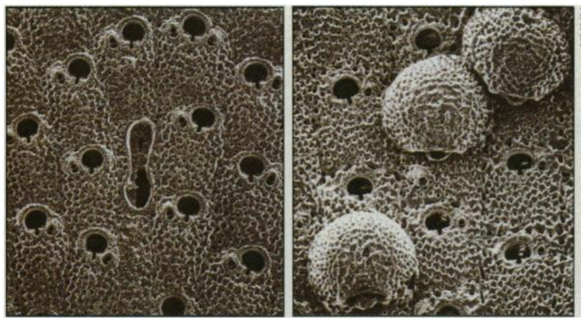
The most thorough study yet of species formation in the fossil record confirms that new species appear with a most un-Darwinian abruptness after long periods of stability

In a 20-year debate about the pace of evolution, paleontologist Alan Cheetham had always known exactly where he stood. Since 1972, when Niles Eldredge of the American Museum of Natural History and Stephen Gould of Harvard University first proposed their theory of punctuated equilibrium, some paleontologists have argued that new species appear suddenly in the geologic record, after millions of years of evolutionary stasis. But Cheetham, like many of his colleagues, thought differently. As a student of the renowned evolutionary paleontologist George Gaylord Simpson, Cheetham had learned that a species changes gradually, through millions of years of natural selection—Darwin's survival of the fittest—until it is so different that it constitutes a new species.

That's the pattern he expected to confirm when he began an exhaustive study of the filigreed remains of corallike animals known as bryozoa, hoping to determine the pace at which new species had appeared during the past 15 million years. But Cheetham, who works at the Smithsonian Institution's National Museum of Natural History, was in for a surprise. "I came reluctantly to the conclusion," he says, "that I wasn't finding evidence for gradualism." What Cheetham did see, again and again, was individual species persisting virtually unchanged for millions of years and then, in a geologic moment lasting only 100,000 years or so, giving rise to a new species.

This just-completed study isn't the first to confirm punctuated equilibrium in the fossil record. But it is the strongest yet, other researchers agree. "Theirs is by far the most complete," says Dana Geary of the University of Wisconsin. Recognizing new species based only on their fossils can be problematic, as critics of earlier studies have emphasized. Cheetham and his collaborator Jeremy Jackson of the Smithsonian Tropical Research Institute in Panama seem to have defused that criticism, at least for the bryozoa, by testing their methods for distinguishing fossil species on living bryozoa. With their study, some paleontologists are now leaning toward punctuated equilibrium as the dominant mode of speciation. "Those who have looked hard, and that's not a large number, have tended to find punctuation," says Geerat Vermeij of the University of California, Davis.

Eldredge and Gould made their original proposal as graduate students, after they had been sent off in search of fossils—Eldredge to upstate New York for trilobites and Gould to Bermuda for land snails—to document the gradual, pervasive evolution that the textbooks said was there. Neither could find it.



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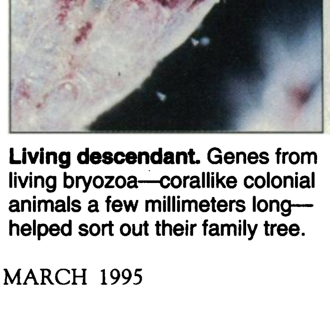
Marks of distinction. Submillimeter skeletal features identify this bryozoan as *Stylopoma spongites*.

Instead they saw species that had gone unchanged for millions of years suddenly give rise to new ones.

Since Darwin, paleontologists have attributed such findings to flaws in the geologic record: The stratum recording the gradual change that led to speciation must simply be missing. But Gould and Eldredge decided to take the fossil record at face value. They proposed that a long-standing mechanism for generating new species—the geographic isolation of a small population of one species for tens of thousands of years—could produce geologically abrupt speciation when the isolation broke down and the new species spread into the rest of the world.

Cheetham, though, regarded punctuated equilibrium as an unnecessary complication, and in 1986 he set out to demonstrate gradualism among the fossil bryozoa he had already spent decades studying. It was awkward for his views that the bryozoan species he was acquainted with did seem to have appeared abruptly. But he was confident that when he made a detailed study of their skeletal features to identify as many different species as he could, gradual speciation would prove to be the norm.



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Living descendant. Genes from living bryozoa—corallike colonial animals a few millimeters long—helped sort out their family tree.

First, with the help of colleagues, Cheetham amassed a large sample of bryozoan fossils of the genus *Metrarabdotos* from the Caribbean and adjacent regions. He meticulously classified them into 17 species using 46 microscopic characteristics of their skeletons such as the length of the individual zooids (the animals that make up bryozoan colonies) and the detailed dimensions of the pores and larger orifices that dot the zooids. Then he arranged them in a *Metrarabdotos* family tree. Yet even though Cheetham's analysis often allowed him to split what had seemed to be a single species into several, the abruptness was stronger than ever. Through 15 million years of the geologic record, these species would persist unchanged for 2 to 6 million years, then, in less than 160,000 years, split off a new species that would continue to coexist with its ancestor species. Cheetham the gradualist "was amazed when he saw the punctuated result that he got," says Jackson.

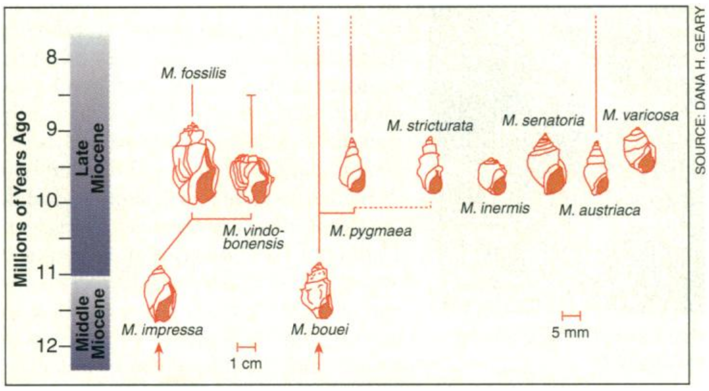
A biological test

Jackson too was impressed, but he wasn't convinced. What if the subtle morphological differences Cheetham was using to split his fossil species really didn't mark separate species at all but rather, say, variants within a species? "Clearly, the strength of any discovery of punctuated equilibrium—a model of speciation—depends on our ability to recognize species," says Jackson. "So I challenged him to submit his methods to biological examination."

As test material, Jackson gathered many different modern bryozoa that are native to the Caribbean. He and Cheetham then tried to distinguish among modern species by applying the same kinds of morphological measurements Cheetham had used for the fossils. The first part of the exam tested consistency: Would the classification depend on how many morphological features they applied? No, the morphological differences that defined 22 species in three distantly related genera of modern bryozoa held up whether Cheetham and Jackson used 20 or 40 morphological characters.

Then came reliability: Do the skeletal details accurately distinguish species? One worry was that the immediate environment might affect skeletal morphology, making populations of the same species living in different environments look like separate species. But when the researchers transplanted bryozoan colonies from different reefs to a single spot, the skeletons of the descendant colonies still closely resembled those of their parents in spite of the changed environment.

Another concern was that morphology might not be a fine enough scalpel: It might lump several different real species into a single apparent "species." So Jackson resorted to genetics. Using protein electrophoresis, he analyzed enzymes extracted from specimens of each of eight morphologically defined species. In each case, all the specimens from each morphological species had much the same enzymes, indicating that they belonged to the same genetically defined species. Cheetham's fossil species had passed the biological test with flying colors.



A favored tempo? The snail *M. bouei (right)* spun off new species in a geologic moment, while *M. impressa* took 2 million years of gradual change.

"Morphology still seems to be a way to say something about the way evolution occurred," says Cheetham. With this confirmation of Cheetham's method of identifying species, Jackson says he "became a believer." He and Cheetham have now extended the earlier work with *Metrarabdotos* to the genus *Stylopoma*. And once again, the 19 different fossil species they traced revealed textbook cases of punctuated equilibrium.

Because of their fastidious identification of species, Cheetham and Jackson's work is widely regarded as the strongest such evidence so far, but it has some competition. Timothy Collins of the University of Michigan and his colleagues, for example, recently took the same biologically based approach as Cheetham and Jackson when they studied a genus of coastal snails called *Nucella*. Although *Nucella* has fewer distinctive characteristics than the bryozoa, Collins and his colleagues also found punctuated equilibrium in the evolution of these snails in California over the past 20 million years.

Those who doubt the importance of punctuated equilibrium, however, can still take heart from earlier studies of fossil freshwater snails by Geary, who documented gradual change within two snail species over periods as long as 2 million years, along with six cases of punctuated speciation. Another verdict of gradual change came from Peter Sheldon of the Open University in Milton Keynes, United Kingdom, who studied morphological change among trilobites from Wales.

Faced with a welter of evidence, some paleontologists are sticking to a middle ground. In *New Approaches to Speciation in the Fossil Record*, the soon-to-be-published proceedings of a 1992 symposium, editors Douglas Erwin of the National Museum of Natural History and Robert Anstey of Michigan State University survey 58 studies published since 1972. They concede that many of these studies have their weaknesses, but they still conclude that "paleontological evidence overwhelmingly supports a view that speciation is sometimes gradual and sometimes punctuated, and that no one mode characterizes this very complicated process in the history of life."

But Jackson, for one, thinks most of the studies supporting gradualism are flawed—for example, because the researchers relied on only a single characteristic to monitor evolutionary change and couldn't be sure they had identified all the species. "I'm imposing pretty strict criteria," says Jackson, "but in the few cases I know [that meet those criteria], it's perhaps 10-to-1 punctuated." Geary, whose work has been used to buttress both sides of the argument, tends to agree. "Gould was my adviser," she says, "but I don't think I have a stake in it. I think that a whole host of patterns is possible, but it does seem to me punctuated patterns predominate."

How to punctuate evolution

If so, evolutionary biologists will feel new pressure to explain how punctuated equilibrium could actually work, a topic about which "there are a lot of hypotheses and not many facts," says evolutionary theorist Mark Ridley of Emory University in Atlanta. One mystery is what would maintain the equilibrium in punctuated equilibrium, keeping new species from evolving in spite of environmental vagaries.

One much-discussed possibility is that species become caught in what Vermeij calls "an adaptive gridlock." Called stabilizing selection, this gridlock results because "there's so much [natural] selection pushing at a species from different directions," Vermeij explains. "It can't go anywhere because moving in one direction has implications for its other competing functions." If a shellfish could reduce the weight of its shell, for example, it might have a better chance of escaping from some fast-moving predators. But that evolutionary route could be closed because a lighter, thinner shell would also decrease its resistance to other predators that bore into their victims. So the species remains unchanged for millions of years until a small population, isolated in a new environment, quickly evolves into a new species.

Stabilizing selection gets some new support in Cheetham and Jackson's chapter in *New Approaches to Speciation in the Fossil Record*. Over millions of years, they point out, any species would be expected to change slightly because of random genetic drift, but their analysis of the *Metrarabdotos* and *Stylopoma* bryozoa suggests something more like evolutionary paralysis. "Our tests strongly favor stabilizing selection" as an explanation of long-term species stasis, says Cheetham.

But that explanation only deepens another mystery: "If stability is the rule, how do you get large-scale shifts in morphology" over many successive species? asks paleontologist David Jablonski of the University of Chicago. "How do you get from funny little Mesozoic mammals to horses and whales? From *Archaeopteryx* to hummingbirds?" One possibility is species selection, a process analogous to Darwin's natural selection but acting at a higher level. A species might be especially likely to spawn new species because of some characteristic of that species that could never appear in an individual, such as having a broad geographic range. As a species wins out in this higher level evolutionary game, Jablonski explains, "all sorts of things get swept along." Body characteristics of individual members of the species, which might have nothing to do with the success of the species as a whole, would turn up in an increasing number of descendant species.

To finally resolve how common such processes are, and how many of his teacher's lessons Cheetham will eventually have to reject, researchers will have to apply a paleontological scalpel as sharp as Cheetham and Jackson's to a variety of organisms, living in many different environments. As Eldredge and Gould have written, "Only the punctuational and unpredictable future can tell."

–Richard A. Kerr

Additional Reading

D. H. Erwin and R. L. Anstey, Eds., *New Approaches to Speciation in the Fossil Record* (Columbia University Press, New York, in press).

J. B. C. Jackson and A. H. Cheetham, "Phylogeny reconstruction and the tempo of speciation in Cheilostome bryozoa," *Paleobiology* **20**, 407 (1994).