pers of 25 infants, the researchers found strains of *E. coli* still resistant to streptomycin, an antibiotic doctors have rarely used for the last 30 years. Adding to this puzzle are bacteria in Richard Lenski's long-term evolution study at Michigan State University in East Lansing. These *E. coli* originally carried a streptomycin-resistance gene called *rpsL*, which is known to markedly reduce the bacteria's fitness. Yet, after evolving in an antibiotic-free environment for 10 years, or 20,000 generations, Lenski's bacteria are still streptomycin-resistant. "Why didn't that gene revert to its sensitive state, when it only required the change of a single DNA base?" asks Levin.

To find out, Levin's colleagues Stephanie Schrag and Véronique Perrot allowed laboratory cultures of *E. coli* with *rpsL* mutations to evolve in an antibiotic-free medium for 16 days, or 160 generations. They then competed these evolved bacteria against drug-sensitive *E. coli* and found that they are almost as fit. "That suggests that they evolved a compensatory mutation," says Levin—a second genetic mutation that makes up for the loss of fitness from the first.

Schrag and Perrot, with Levin and Nina Walker, confirmed that suspicion by making their evolved *E. coli* strain drug-sensitive again. They replaced the bacteria's streptomycin-resistant *rpsL* gene with a sensitive version of the gene, then set this genetically altered strain and the resistant strain against each other in another fitness-competition bout. The genetically altered *E. coli* failed miserably—implying that the compensatory mutation reduced its fitness when not paired with the resistance gene.

The interaction between the two mutations would act as a kind of ratchet, preventing bacteria from reverting to sensitivity. "The compensatory mutations establish an 'adaptive valley' that virtually precludes that population of resistant bacteria from returning to drug sensitivity," explains Levin. And that explains why the bacteria in Lenski's lab and possibly those in the children's diapers have not lost their resistance. "Those that revert, that make that one change, are at a disadvantage," explains Levin. The team is now trying to identify the gene that carries this compensatory mutation.

Levin suspects that the same kind of compensatory mutations "will almost certainly be found in other resistant bacteria." But already, the findings have "clear, practical—and rather frightening—implications," says Marlene Zuk, an evolutionary biologist at the University of California, Riverside. "It's not enough to stop using antibiotics; the bacteria aren't going to revert to what they were before"—and antibiotics that have lost their effectiveness won't become powerful weapons again.

–Virginia Morell

PALEONTOLOGY

Does Evolutionary History Take Million-Year Breaks?

The history of life is one continuous upheaval, or so strict Darwinists would have it. Species come and go continually, as creatures either adapt to a changing environment and ever-shifting competition and evolve into new species, or become extinct. But lately, a small group of paleontologists has been asserting that evolution sometimes takes a holiday. In the fossil record of hundreds of millions of years ago, they point to examples of entire communities of marine animals that remain snared for millions of years in something close to stasis, then plunge into a brief frenzy of extinction and new species formation.

Claims of such "coordinated stasis" have galvanized the paleobiology community into a frenzy of its own as researchers try to test the idea by studying how other animal communities fared over tens of millions of years. The first results to come in are "a mixed bag," concedes paleontologist Carlton Brett of the University of Rochester in upstate New York, who, with Gordon Baird of the State University of New York, Fredonia, first proposed the concept of coordinated stasis in 1992, based on 400-million-year-old marine fossils from New York. "The pattern we have seen is holding up well in our rocks," he says, but "that pattern is perhaps toward the extreme end of a range." Indeed, most studies of similar fossil records have found little evidence for prolonged periods of evolutionary stasis.

C. BRETT/UNIV. OF ROCHESTER

Where's the evolution? Not much happened to these common marine species over a nearly 10-million-year interval (*bottom to top*) roughly 400 million years ago.

Yet confirmation of even occasional episodes of coordinated stasis in the fossil record could have major ramifications for understanding evolution. One proposed explanation for the stasis is that the species in the static ecosystems interacted so tightly that there was no room for change. If so, the more fluid ecosystems of recent times, in which individual species react independently to evolutionary pressures, may not be the evolutionary norm. The brief upheavals of accelerated evolution said to begin and end the periods of stasis are more widely accepted, but just as intriguing, hinting at little-understood evolutionary dynamics (see sidebar).

The classic case of coordinated stasis comes from the animals that lived in ocean-bottom muds during the early Silurian to middle Devonian periods, about 440 million to 380 million years ago. Those muds hardened into fossil-bearing shales that are now found in Ontario, New York state, and Pennsylvania. Studying the rocks nearly a century ago, paleontologist Herdman Cleland noted that the array of fossil species, including the mollusklike stalked brachiopods, corals, mollusks, echinoderms such as starfish, and trilobites, seemed to change very little over many millions of years.

It was not until the early 1990s that Brett and Baird, drawing on fossil specimens collected over 20 years, quantified the stability that Cleland had reported. They identified 14 intervals, generally running 3 million to 7 million years each, during which 60% or more of species persisted with little change. Within each interval, extinction, speciation—the formation of new species—and immigration of species from outside the now-vanished ocean basin were all more or less on hold, until the interval ended in a period of drastic turnover lasting just a few hundred thousand years.

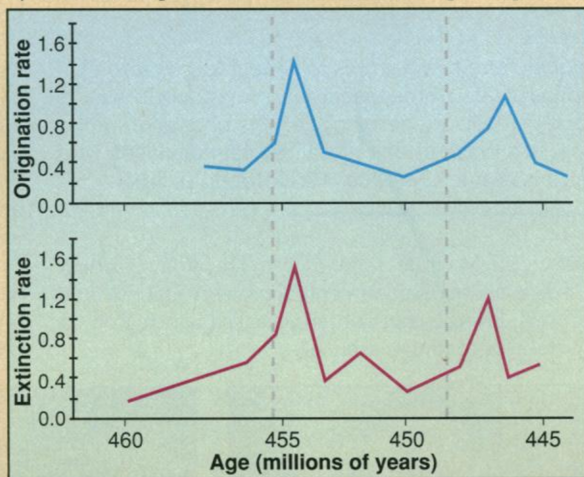
The herky-jerky pattern hearkens back to the revolutionary concept of punctuated equilibrium proposed by Niles Eldredge of the American Museum of Natural History in New York City and Stephen Gould of Harvard University in 1972. They argued that species tend to persist unchanged for millions of years before abruptly giving rise to a new species, instead of evolving gradually. Coordinated stasis "is punctuated equilibrium at a higher level, the ecological level of the community," says Douglas Erwin of the National Museum of Natural History in Washington, D.C. But while there is finally some strong evidence for the reality of punctuated equilibrium (*Science*, 10 March 1995, p. 1421), many paleontologists have had a hard time swallowing the idea that all the species in a community could be held in check at once.

Even more startling was the explanation for coordinated stasis advanced by Paul Morris of the Paleontological Research Institution in Ithaca, New York, Linda Ivany of the University of Michigan, Ann Arbor, and Kenneth

When Evolution Surges Ahead

While paleontologists poring over their records of ancient sea creatures debate whether the evolutionary turnover of species ever slows toward stasis (see main text), they do agree that every few million years, it can speed up dramatically. All three studies done to test the idea of stasis in 400- and 500-million-year-old communities of mollusklike brachiopods showed these evolutionary "events." So did studies of 500-million-year-old trilobites and 300-million-year-old crinoids—stalked marine animals that look like flowers.

These events fall well short of the species turnovers that follow global mass extinctions, every hundred million years on average: They are more frequent and may be limited to a single ocean basin. But in each one, upwards of 60% of species seem to be replaced over a period of a few hundred thousand years. At least some of these boundary events could be artifacts of the geologic recording process, says Steven Holland of the University of Georgia, Athens. At times when sea level falls rapidly, he says, a dearth of sediment deposition can compress the geologic record in shallow-water sediments, making the evolutionary clock seem to speed up. But by examining the events in sediments from deep water as well as shallow, he and Mark Patzkowsky of Pennsylvania State University have identified at least one event about 455 million years ago that is clearly real.



All together now. The pace of new species formation and extinction surged at the same times in the east-central United States about 450 million years ago.

Now the question is what triggered this and other surges. Holland and Patzkowsky identify several possibilities in the environment. Their studies of the sediments that record the evolutionary surge show a drop in sea level, a change in ocean circulation, and perhaps a change in water temperature. In general, "it looks like the coincidence of several rapid environmental changes is what undoes the system," says paleontologist Carlton Brett of the University of Rochester in New York state. Together, he suggests, the changes push organisms so hard that they cannot adapt or move to more suitable conditions fast enough. As a result, leisurely change—or outright stasis—gives way to upheaval. –R.A.K.

Schopf of Harvard in 1995. They proposed that the ecological interactions among species—those that compete, prey on each other, or depend on each other—might have been so specific and intricate that a new species or an invader from outside the community could not break in. This interdependence was so strong, they suggested, that even if the community came under pressure from, say, climate change, it might not change—instead, it might shift en masse to a more suitable environment in deeper or shallower water. That kind of interdependence has no parallel in modern ecosystems, which constantly reorganize in the face of environmental change.

Prompted by this provocative hypothesis, paleontologists are now searching for stasis in their own data sets, with mixed results. During the past 10 years, Mark Patzkowsky of Pennsylvania State University and Steven Holland of the University of Georgia, Athens, noted the comings and goings of brachiopod species in a roughly 20-million-year interval of the Ordovician period about 450 million years ago, as recorded in rocks in Tennessee, West Virginia, and Virginia. "Of all the studies out there, ours is most similar to Brett and Baird's," says Patzkowsky. "Do we have the same pattern?" he asks. "The answer is no."

The record does include some intervals when evolutionary churning slowed, but even then the rates of speciation and extinction "are much higher than what Brett and Baird report," says Patzkowsky. Fewer than 10% of the late Ordovician species persisted through an interval, compared with 60% in the Devonian. Stephen Westrop of Brock University in St. Catherines, Ontario, found similar patterns in the trilobites late in the Cambrian period, 520 million years ago.

But the news for coordinated stasis is not all bad. Mark Harris of the University of Wisconsin, Milwaukee and Peter Sheehan of the Milwaukee Public Museum inventoried species in a brachiopod-dominated community from about 430 million years ago, early in the Silurian period just following the Ordovician. "The story's very similar to that in the Devonian of New York," says Sheehan.

To Schopf, the mixed findings suggest that "different parts of the fossil record may show this pattern more clearly than others. Some parts may not show it all." Some paleontologists see an exciting implication: The rules of the ecological game that enforced stasis may have changed over time, locking up ecosystems at some times but not others. Westrop, however, thinks the sporadic appearance of stasis implies that it is an artifact, appearing when the ecosystem is dominated by a group of animals in which individual species happen to be unusually resistant to extinction. For example, a species whose larvae disperse widely because they are free-floating in the sea should endure longer than one whose less mobile offspring could be wiped out by a local disaster. Westrop thinks he sees examples of a species duration effect in the Cambrian: The trilobite community, made up of typically short-lived species, was relatively unstable while brachiopods, which had longer species durations, were more stable.

No one expects paleontologists to agree anytime soon on how common coordinated stasis is or what accounts for it. "Everybody's data sets aren't quite comparable," says Patzkowsky. "They're from different times, the rocks are different, the rock exposures are different, the animals are different. It makes it difficult to compare patterns." And repeating any one of these massive studies would take a decade of a researcher's time and would mean infringing on another paleontologist's field area. The best hope, says Patzkowsky, is "a more consistent comparison of data sets," using procedures that limit the number of variables, including the inevitably subjective process of defining species in the fossil record.

Brett, who started it all, thinks there will be at least one sure payoff. "I think the idea of coordinated stasis has stimulated a lot of people to look at the record more closely," says Brett. "Maybe that's the main benefit of it all."

–Richard A. Kerr

Additional Reading

Special issue on "New Perspectives on Faunal Stability in the Fossil Record," L. C. Ivany and K. M. Schopf, Eds., *Palaeogeography, Paleoclimatology, Paleoecology* **127**, 1–359 (1996).