Evolution Made Visible

Charles Darwin didn't think you could watch evolution in action. But modern biologists are getting a good look at processes such as natural selection and even at the origin of species

For all his experiments with earthworms, orchids, hawks, and ferns, Charles Darwin never tried to watch evolution happen. In fact, he didn't think that was possible. The process works "silently and insensibly," he wrote in *The Origin of Species*. "We see nothing of these slow changes in progress, until the hand of time has marked the lapse of ages."

And that view hasn't changed much. Even today, most people picture evolution as a drama that cannot be tracked in real time, a production so ponderous that it takes hundreds, thousands, or millions of years to see any action at all.

But in the last two decades, evolution has become highly visible. Computers now allow scientists to store a lot of numbers and work through them quickly, detecting physical changes as whole populations move from generation to generation. The tools of molecular biology allow investigators to track some of these changes at the level of DNA. And some of the same investigators have devised ingenious experiments—many in natural settings—to highlight such changes.

As a result, ideas about evolution that have long been speculative are being bolstered by experimental data for the first time. Two months ago, for instance, Dolph Schluter of the University of British Columbia in Vancouver reported on a population of stickleback fish that began to change shape and feeding habits when a new competitor forced the fish toward a different ecological niche (*Science*, 4 November 1994, p. 798). Evolutionary biologists have long contended that competition has the power to do this—to shape the future of a population, or even an entire species—but the evidence, much of it from fossils, has been indirect and, to many, unsatisfying.

This new version of evolution made visible is getting rave reviews. "It's just a great paper. It's a remarkable result," says Stuart Pimm of the University of Tennessee of the stickleback work. "In ecology and evolution, we see the results of processes, and we argue about how the results came out as they did. It is always hard to infer process from pattern.

The ways and means of evolution are the topics of this special news report. First, we report on real-world evolutionary processes unfolding before observers' eyes, in real time. Next comes a story on how the algae fossil record is revealing unexpected bursts of species change early in life's history, and the possible reasons behind this. In human history, one of the big questions is why our species seems remarkably uniform genetically; our final story reports on evolutionists' efforts to solve this puzzle.

A related Perspective appears on page 41, and a related Report begins on page 87.

There's often a lot of uncertainty. Now people are getting very clever in coming up with intelligent and sensible ways of getting at the underlying process."

One of the most prominent researchers to explore evolution in this way is John Endler of the University of California, Santa Barbara. Twenty years ago Endler began to watch the interplay of two evolutionary forces, natural and sexual selection, as they drove changes among populations of guppies. Natural selection is the process by which the environment picks and chooses among the living; sexual selection is the process by which the living pick and choose among each other. The two processes sometimes push and pull living things in opposite directions.

Starting something new. Two species of Galápagos finches *(top and bottom)* are mating and producing hybrids *(center)*. These fertile hybrids could be the start of a new species; hybridization could be more important in animal speciation than scientists had previously thought.

PHOTOS BY P.R. GRANT

The tug of selection

Endler's guppies, for example, felt those opposed pulls in the streams of Venezuela's Paria Peninsula and Trinidad's Northern Range. In the sections of those streams where the guppies were endangered by predatory fish, the guppies' colors blended with the sand on the streambed for camouflage. In safer waters, however, the guppies had more visible colors, with spots bigger than the sand grains. Endler thought the first situation should be the result of natural selection—guppies that didn't blend in would be eaten—while the second stemmed from sexual selection: Standout fish should be more attractive to females and get more chances to mate.

In the 1970s, to test this hypothesis, Endler built artificial streams in the laboratory and seeded them all with guppies and some with guppy-eaters. Within only 5 months (nine or 10 guppy generations), the guppies in the artificial streams had evolved precisely as predicted. In the dangerous streams the males changed to blend in better with the background, and in the safe streams they became more conspicuous.

Endler also tried the experiment in the wild. He moved 200 guppies from dangerous waters to much safer waters 2 kilometers away. Within a year, the descendants of those 200 guppies had changed. Compared to their blend-in cousins in the dangerous stream, they were now standouts. It was a clear demonstration of these evolutionary principles in action.

Today, Endler is using the guppies to test other ways that sexual and natural selection can tug at an organism. In 1930, Ronald Fisher, then at Rothamsted Experimental Station (U.K.), pointed out that sexual selection puts pressure not just on males, but also on females. The females that choose the most attractive males will tend to have the most attractive sons, sons that will pass on more of the family genes. So wherever males court females, the females who can make the finest discriminations among the males' displays should do best, genetically speaking. As females evolve greater powers of discrimination, Fisher suggested, they put pressure on males to refine or elaborate their displays; the better the male displays, the more selective the females should become. In theory, this process could "run away" and produce spectacular displays like the tail of the peacock or the song of the male humpback whale.

Endler and others are interested in identifying the initiating event. In a process Endler calls "sensory drive," biases in the animals' sensory systems could favor one sexual signal over another. These biases could help to shape the male trait that becomes the object of female desire.

In 1991, Endler and Alix Basolo began trying to set off one of these episodes among his guppies. They began with an artificial selection experiment: They bred individual female guppies whose color vision tested strongest in red and blue. This stage of the experiment is now complete. "We've gotten a very strong response," Endler says. "Very strong response in the red and the blue, and no change in the controls. We're now in generation eight."

Now comes the real test. Will the females, with their altered color vision, begin to choose the males with the brightest blue or the brightest red? If they do, they may force an evolutionary change in the males' color patterns. Thereafter, the change in the males may force the females' color vision to change even more, so that the changes on both sides begin to "advance together," as Fisher said. If they begin to "run away," then Endler and Basolo might be able to predict the direction that evolution might go. They hope to run the experiment for 20 or 30 generations.

If Endler and Basolo succeed, it would be the first demonstration of sensory drive, a phenomenon often debated by evolutionary biologists, in action. "That would be absolutely fascinating," says Douglas Futuyma of the State University of New York, Stony Brook. "I'm certainly in the camp that finds the sensory drive process very intriguing. And there's some circumstantial evidence. But having an experimental demonstration always makes you more confident."

The competitive edge

Sometimes the selective pressure driving change in a species comes not from a mate or predator but from a crowded ecosystem. This is what Schluter is investigating. Schluter studies threespine sticklebacks (*Gasterosteus aculeatus* complex) that were cut off from the sea and trapped in small glacial lakes in British Columbia at the end of the last ice age, about 12,000 years ago. Wherever two stickleback species share a lake, it turns out, one species always feeds on the bottom and the other feeds above it in the water column. Benthics—the bottom-dwellers—have bigger, fatter bodies, with wide mouths and coarse food filters (spiny sieves in the gills). Limnetics—which feed higher up—are smaller, thinner, with narrow mouths and fine food filters. But if one species is alone in a lake, it is a generalist with an intermediate body type and intermediate filters, and it feeds all over the place. "This pattern is repeated in lake after lake," Schluter says. "It's hard to see the pattern unless you've got it repeated."

Crowded out. Stickleback fish that feed high in a lake's water column are forced out of a population by competitors with similar feeding habits.

The classic explanation for this evolutionary pattern is based on competition. Almost 40 years ago biologists William Brown Jr. and Edward O. Wilson pointed out that when closely related species live side by side they are often specialists, adapted to slightly different niches. Brown and Wilson thought that species with very similar original characteristics might have evolved to keep out of each other's way. Brown and Wilson called this pattern "character displacement." The benthics and limnetics appear to be a neat example.

But again, observed pattern does not equal observed process. Ecologists such as Daniel Simberloff of Florida State University have pointed out that without seeing the events that led up to the present situation, alternate explanations are possible (*Science*, 12 August 1983, p. 636). For example, the two fish species might have started out with different food preferences.

So Schluter decided to speed up evolution. First he collected sticklebacks from a lake near the university, Cranby. In Cranby there is only one species of stickleback, and it is a generalist, neither benthic nor limnetic. Then, on campus, Schluter divided an artificial pond in half. He put 1800 young Cranby sticklebacks in side A. He put another 1800 in side B, but also added 1200 young limnetics from another lake. He let all the fish grow for 3 months (they take a year or two to reach full size), and then he began taking measurements and crunching the numbers in his computer.

In side A, with no competition, the Cranby generalists grew much as they do in Cranby Lake. But in side B, the generalists that were most like their competitors—the most limnetic in body and behavior—grew more slowly than did the individuals that were more benthic. In a second experiment, more crowded with limnetics, these growth rates were even further suppressed. Natural selection was starting to favor the generalists with benthic leanings: They had less competition for food, and they matured more quickly. In the future, Schluter hopes to determine if these fish produce more offspring. If their offspring turn out to be more benthic as well, then a whole suite of characters will have been displaced.

"It's a remarkable result," says Pimm, "because this process is a key mechanism in the origin of species. We all have the idea that isolated populations will diverge. But what happens when they are brought back together? It's not obvious that they will be driven apart. They could also mix together and hybridize. Schluter's experiment is a very simple and elegant demonstration that it really does happen that the two lines are forced apart. There was not a great deal of evidence for that before Schluter's paper."

Crossing the species line

Another team of researchers watching mechanisms involved in the origin of species is doing it where Darwin began: the islands of the Galápagos. Peter and Rosemary Grant of Princeton University have been watching the effects of seed size on the beak shapes of Galápagos finches since the early 1970s, and they have seen that changes in the type of available seeds produce changes in beak size—a genetic trait—within a single year, from one generation to the next. It's a modern classic in the study of evolution in action. Now, focusing on finches on the tiny desert islet of Daphne Major, the Grants are trying to make sense of a new twist in the birds' evolution.

A medium-beaked ground finch, *Geospiza fortis*, one of several finch species that breed on the island, is breeding with *G. fuliginosa*, the small-beaked ground finch, and with *G. scandens*, a cactus finch. These three species did sometimes interbreed in the early years of the Grants' study (two or three cases in a hundred), but none of their offspring lived long enough to reproduce. While interbreeding is still as rare, many of the hybrids are now surviving (*Science*, 10 April 1992, p. 193). All this interbreeding is increasing the finches' variability, creating new morphological types—and presumably new combinations of genes behind them—on Daphne Major. "A gene that starts off in one species can finish off in another," says Peter Grant.

Under certain conditions, crosses between species—hybridization—can lead to the origin of species. Botanists believe that about half (some say more than half) of the plant species on the planet formed through hybridization and isolation of the new genetic population.

Hybridization is supposed to be a rare occurrence among animals. But the Grants are learning that it may, in fact, play an important role in animal evolution. A few of the Daphne Major hybrids are the fittest finches on the island: They are producing the most offspring and sending the most copies of their genes into the next generation. Although these hybrids haven't yet become a breeding population unto themselves, there are many ways they could, and that would signal the beginnings of a new finch species. "If the hybrids fly off to a new island, or if they backcross to one of the parental species and their offspring are very fit, the population will be altered in a new direction, and perhaps go off on a new evolutionary trajectory," Peter Grant says.

Sex: Variations on a theme

The origin of species is not the only question that intrigues evolution-watchers, of course. They are also looking for answers to the longstanding mystery of sex. Sexual reproduction involves time, effort, and risk—think of Endler's guppies. Asexual reproduction, or cloning, involves less of all three, with the added benefit that all of a parent's genes get passed down to each offspring instead of only half. So asexual creatures should outcompete sexual ones and drive the sexual ones to extinction. But they don't. There are even species of animals—including certain moths, frogs, lizards, and topminnows (plain little fish that live in desert arroyos of northern Mexico)—in which some lines reproduce sexually, others asexually. What do the frogs, the topminnows, and the rest of us get out of sex?

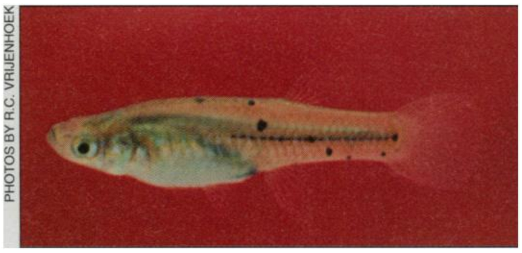
The theoretical answer has been variability, produced by the new combinations of genes arising from sexual reproduction. According to a hypothesis put forward by Leigh Van Valen of the University of Chicago, genetic variability gives sexual organisms an advantage in the struggle for existence because it makes them moving targets for parasites and predators. By shuffling the genetic deck in each generation, sexual species keep dodging their enemies (although their enemies keep evolving too, the better to prey upon them). Asexual clones, in contrast, are by and large stuck. They are genetically monotonous and can't adapt to changing times. Van Valen calls this the "Red Queen hypothesis," because in this view all sexual beings are like the subjects of Lewis Carroll's Red Queen: "Now, here, you see, it takes all the running you can do to keep in the same place."

Like so many other ideas in evolutionary biology, the Red Queen hypothesis has been conceptually appealing but difficult to test; the arguments for it rest on logic and inferences. But now Robert Vrijenhoek, director of the Center for Theoretical and Applied Genetics at Rutgers University, has made some compelling observations that flesh out the Red Queen's logic. Since 1975, Vrijenhoek has been tracking the evolution of topminnows (genus *Poeciliopsis*) in the American Southwest. These fish make particularly good tests of the Red Queen hypothesis, because very often, asexual and sexual species of topminnows share the same desert pool.

In these pools, flatworms often burrow into the body walls of the fish, giving them black spot disease. Vrijenhoek, who analyzed the fish DNA to determine genetic similarities and differences, has discovered that in pool after pool the race against black spot disease follows the pattern predicted by the Red Queen: The most common clone is the one that gets hit worst by the flatworms. The less common clones do better. The sexual species do best.

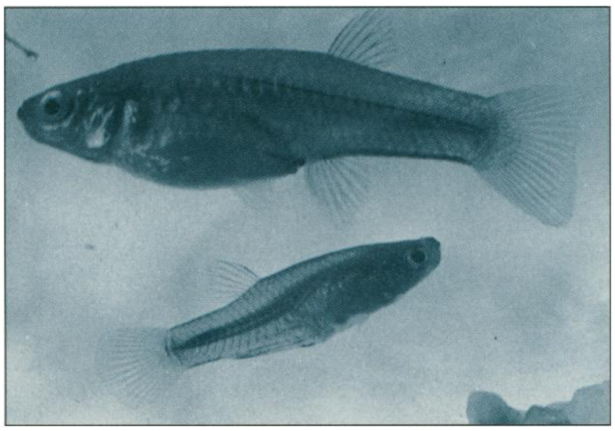
About the time he began his observations, Vrijenhoek witnessed an odd reversal of fortune that gave further support to the Red Queen. In 1976, during a severe drought, some of the pools and streams that Vrijenhoek and his students were studying went dry. By the spring of 1978, rains had refilled these pools, and topminnows swam up from downstream. But only a few sexual topminnows reached the new pools, and their progeny were all very much alike. So the sexual fish in the pool had lost most of their genetic variation. In fact, they were so inbred that they had less genetic variation than did the clones in the same pool. Success followed genetic variation: The inbred sexual line contracted black spot disease more often than the clones did and remained rare.

When Vrijenhoek added 30 sexual, genetically variable female topminnows to one of these pools, however, their genetic diversity rebounded. Now once again the sexual topminnows were the ones that were generally spared the ravages of black spot disease, and once again they outnumbered the clones. To this day they are the top minnows in their pool.



PHOTOS BY R.C. VRIJENHOEK

Spotting a clone. Black spot disease attacks topminnow species with the least genetic variation, such as this one.



Sexual surprise. This new and unnamed topminnow species reproduces sexually—although it evolved from an asexual species.

Vrijenhoek's studies show how crucial genetic variation can be to the survival of a line—a demonstration that has value not only for evolutionary biology but for conservation biology as well. And survival is becoming a pressing issue for the topminnows. Their habitats are fragile drainage areas, no more than slight trickles of water for most of the year. Now these areas are being disrupted by dams and by exotic fish such as black bass and cichlids. It remains to be seen whether topminnows have enough variability to adapt to these latest challenges; the scientists who work with them are pessimistic.

But evolution continues. Other evolutionists are watching Soay sheep on the island of St. Kilda, lions in the Serengeti, and mice in the horse barns of Princeton. Still others are looking at evolution in the lab. In experiments reported on page 87 of this issue, Michael Travisano of Michigan State University and his colleagues studied changes in populations of *Escherichia coli* in an effort to untangle the effects of adaptation, chance, and the historical limits imposed by a progenitor's genes. In one experiment, they took a single population and used it to found 12 new populations, which they raised for 2000 generations in separate but identical environments. Within these 12 populations, some traits evolved and diverged, while others stayed the same. Next, the experimenters used the 12 populations to found 36 new ones, and raised them all in a new nutrient environment for 1000 generations.

The question: Would the populations' prior histories constrain their evolution, or would chance push them in different directions, or would all 36 adapt in a similar way to the new conditions? The answer: In one important trait—the ability to reproduce faster than a rival group—the 36 groups converged dramatically, despite different starting points. They would not have done this by chance, or because of historical limits. But in another trait, cell size, they continued to diverge, indicating a stronger role for chance. "There's been a lot of debate about trying to untangle history, chance, and adaptation," says Richard Lenski, a co-author on the paper. "And this shows that in the proper setup, you can rigorously quantify the different effects."

All evolution watchers, however, learn to expect the unexpected. Vrijenhoek was recently surprised to learn that topminnow asexual clones are not necessarily evolutionary dead ends. Last year, he discovered a new topminnow species that has arisen from an asexual clone. "The new species reproduces sexually, has a 1:1 sex ratio, and has a unique niche," Vrijenhoek reports.

"How did it happen? Don't know," he says with a laugh. He notes that sexual species can give rise to asexual ones through a mutation that disrupts meiosis—the division of chromosomes that allows the production of sex cells—and speculates that in this case, another mutation restored the function. The new species, not yet named, feeds on the larvae of certain midges in the marshes of its river basin. The river is called, appropriately, the Rio de la Concepción.

–Jonathan Weiner

Jonathan Weiner's latest book is The Beak of the Finch *(Knopf, 1994)*.

Additional Reading

J. A. Endler, ***Natural Selection in the Wild***, Monographs in population biology, Princeton University Press, 1986.

EARLY LIFE

Timing Evolution's Early Bursts

Life's evolutionary engine seems to have been stuck in idle for much of the first 3 billion years of its existence. As late as a billion years ago, the single-celled algae floating in the oceans were stagnating in simple species. But then, according to a new survey of the fossil record, the pace of evolution among these algae quickened noticeably. And at about the same time, as the genes of living species show, the evolution of the unknown, unfossilized creatures that gave rise to animals took off too.

How was the evolution of such disparate creatures as algae and animals jump-started? Paleontologist Andrew Knoll of Harvard University can't prove it, but his newly detailed fossil record of changes among species of planktonic algae, published this summer in the *Proceedings of the National Academy of Sciences*, suggests a promising possibility: that something new in the genes, perhaps the ability to reproduce sexually, could have spurred that first surge in plants and animals.

"Andy has proposed a nice hypothesis, a first attempt to put all of the molecular data together with the geological data," says Jere Lipps of the University of California, Berkeley. "There are going to be improvements as we go along, but all of us are coming around to a general perception that's similar." Although the geologic record of the early evolution of life is skimpy, and the molecular record provides only sketchy hints about timing, the combination of the two is providing paleontologists with a new tool for dating and characterizing evolutionary bursts—and for theorizing about the causes behind them. Knoll's approach is yielding insights not only into this early evolutionary burst, but also into the "big bang" that followed it: the Cambrian "explosion" of 500 million years ago, when simple animal forms were supplanted by a variety of clawed and armored body types that still exist today.

But it's the window into the pace and timing of evolution during the great stretch of time before the Cambrian that is drawing a lot of attention. Paleontologists have long struggled to measure evolutionary change during this 2-billion-year period, known as the Proterozoic, but their analysis has been stymied by the lack of hard-shelled animals that fossilized well. There are fossils of groups such as the blue-green algae, but only rare ones that don't provide a complete track through time.

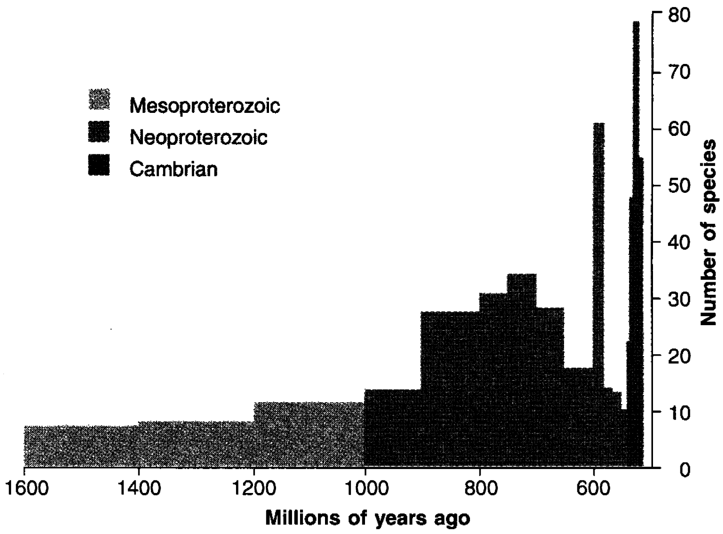
Knoll, however, has long felt that single-celled planktonic algae could serve as guideposts. These algae were encased in microscopic, organic-walled vesicles that endured to be preserved in profusion in Proterozoic rocks around the world. Their increasingly varied size and ornamentation allows tracking of the direction and pace of evolution as new species appear and old species go extinct. "It is the one record we can look at in the Proterozoic that is likely to be dominated by an evolutionary signal," says Knoll.

To follow the signal in this record, Knoll has, over the years, amassed the best collection of such fossil-bearing rocks in the world. "He's visited or has samples from most of the potential localities in the world," notes Proterozoic paleontologist Jack D. Farmer of Ames Research Center in Mountain View, California. The collection has given Knoll the chance to classify all his microfossils himself—a tremendous advantage in tracking changes in species through time, says Farmer. The alternative is to rely on the opinions of others in the literature, and one person's yardstick of species changes—judgments based on the extent of alterations in shape, for instance—may not match that of another observer.

The first planktonic algae appear in the geologic record 1.8 billion years ago, representing the first appearance of eukaryotes, or cells bearing a nucleus. According to Knoll's data, there were five or so algal species to start. And most of those species hung around, barely changing, for the next 800 million years. During more recent times—the past half-billion years—evolutionary change has been much more rapid: Algal species persist for only 5 to 10 million years before becoming extinct.

Then, as life entered the billion years leading up to the present, the evolutionary pace picked up dramatically, according to Knoll's analysis. More and more new planktonic algae species began appearing, and, more important, species turnover—the extinction of existing species and the appear-

ALGAE ACROSS TIME



Accelerating evolution. After a long lull, the number of planktonic algae species shot up 1 billion years ago. A burst also followed the Varanger ice age about 600 million years ago, then the Cambrian "explosion" hit.