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

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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.

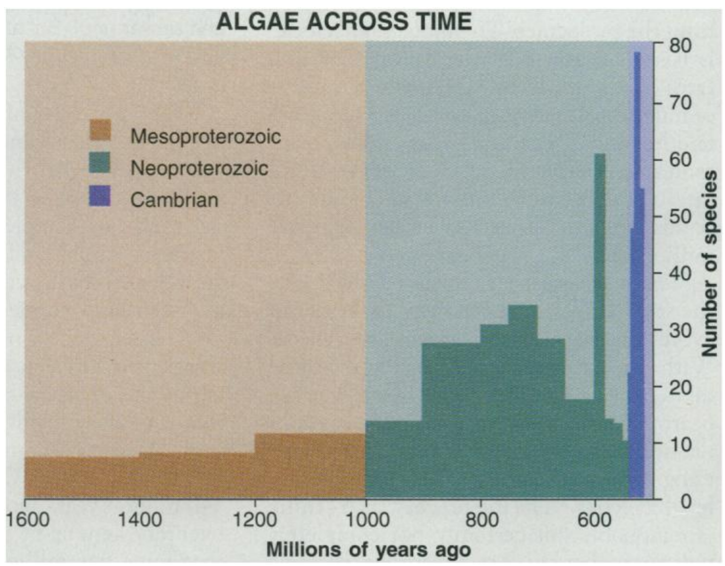
But it's the window into the pace and timing of evolution during the great stretch of time before the Cambrian that is drawing a lot of attention. Paleontologists have long struggled to measure evolutionary change during this 2-billion-year period, known as the Proterozoic, but their analysis has been 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-



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.

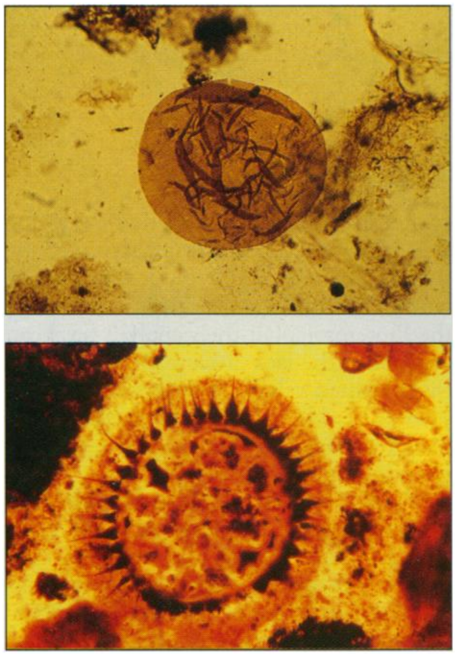
ance of new ones—increased by a factor of 10. On average, a species only persisted for 100 million years, a turnover rate far short of recent times but a hefty acceleration over the nearly 1-billion-year average life-span of the earlier groups. In addition, paleontologists such as Nicholas Butterfield of Cambridge University, along with Knoll, have in the past 5 years found rare fossils of multicellular algae—the green, red, and brown algae—that first show up in the record 1 billion years ago, the same time as the planktonic algae take off.

What got algal evolution out of its rut? Knoll doubts it was anything physical. "No one has as yet identified a major environmental change a billion years ago that might have provided a driving force," he says. "One has to look to features of biology that are not preserved in the geologic record."

Some of these features, he thinks, are the DNA and RNA sequences that are preserved in living creatures. The more similar the sequences of one species are to another's, the more closely related they are. Researchers such as Mitchell Sogin of the Marine Biological Laboratory in Wood's Hole, Massachusetts, have used ribosomal RNA (taken from the cellular organelles used to construct proteins) to build a family tree of life that reveals a sudden explosion of evolution on the branch carrying the nucleus-bearing eukaryotes. All manner of new eukaryotes suddenly came into being at about the same time, including the multicellular algae and the ancestors of animals. But just what "time" that was is hard to discern from the molecules. The molecular "clock" is based on applying the known mutation rates of the ribosomal RNA to the number of mutations that separate one species from another and calculating backward to a common ancestor. But this clock is not very accurate. All that can be said for sure is that its hands point to a time longer ago than 500 million years.

That's where the geologic record comes in, says Knoll. It too points to bursts of evolution, but with better time resolution. With the turnover rate of planktonic algae taking off and multicellular algae first appearing a billion years ago, Knoll sees a connection between this schedule and the flowering of eukaryotic forms read from the molecular record. "The inference, which I think is reasonable but certainly not completely proven, is that these two histories [geologic and molecular] are telling us about the same event," he says.

And the molecular history may contain some clues about the provocation for this event. Some sort of fundamental genetic innovation seems like a good prospect, says Knoll. In the molecular record, groups that now have fully meiotic sexual reproduction—in which separate sex cells, such as egg and sperm, are produced through a process that enables chromosomes to divide and recombine—did not appear until after the big eukaryotic explosion. The opportunity to shuffle and reshuffle genes would have increased the variability of the eukaryotes' genetic makeup. Such variability in turn would have expanded the possibilities for evolutionary innovation. With that capability, notes Knoll, the tempo of evolution could have picked up.


PHOTOS BY A.H. KNOLL

Life gets complicated. Earlier than 1 billion years ago, most planktonic algae were simple and similar *(top)*. But after that time, complexity and diversity set in *(bottom)*.

Lipps says the confluence of the two lines of evidence clearly indicates something new was happening in these creatures. And he finds the sex angle intriguing, although he says he's not completely persuaded. Some major environmental change, possibly a rearrangement of the continental land masses, might still have done the trick.

Neither genes nor environment, but competition, may have helped drive the last big evolutionary burst reflected in Knoll's record of algae fossils: the Cambrian explosion. Diversity among the algae once again doubled in the early Cambrian period, about 540 million years ago, and the species turnover rate went up by another factor of 10. In that same few million years, animals were appearing in the fossil record in a profusion of new forms that ended the Proterozoic and set the direction of evolution for the rest of time. The leading explanation for the animals' diversification has been rising atmospheric oxygen levels, marked by the increasing storage of carbon in ocean sediments. But Knoll reasons that if organisms as different as microscopic, photosynthetic algae and macroscopic animals like trilobites and starfish were emerging at the same geological moment, there must have been more to it than oxygen. Animals presumably needed more oxygen to become larger and more active—but the algae didn't.

"This rapidly increasing [Cambrian] diversity, I suspect, is in no small part a product of spiraling ecological relationships," says Knoll. Farmer agrees. "Organisms assist in creating their own environments," he notes. "If you invent a new ecology, you can bet you're going to affect evolution. There are additional loops within the [expanded] system that can be exploited by other groups of organisms." Such loops in the Cambrian explosion, and in later evolution, might have included enhanced recycling of nutrients as proliferating animals found ways to return nitrogen and phosphorus to new parts of the water column, where new forms of algae might evolve to exploit them. And new kinds of algae might in turn have provided new sources of food for animals able to evolve the ability to take advantage of them.

Diversity, however, does seem to have a price. As William Schopf of the University of California, Los Angeles, has pointed out, since the Cambrian Period, life and the ecosystems it formed have been complex but precariously poised. Largely as a result of ecological specialization arising from eukaryotic diversification, says Schopf, much of life became susceptible to repeated episodes of extinction, a half dozen of which have been of disastrous proportions.

A foretaste of such disasters—the first mass extinction ever recorded—is clearly revealed in the algal fossil record. A spike in planktonic algae diversity, first recognized by Wenlong Zang of the Australian National University, falls between the pulse at 1 billion years ago and the Cambrian explosion. After shooting toward peak Cambrian levels, the species diversity just as quickly collapsed. Seventy-five percent of the recorded algae species disappeared, according to Knoll's record. A major glaciation, the Varanger ice age, immediately preceded the spike at about 600 million years ago, but Knoll won't speculate on any cause-and-effect relationship between the two events. The algae record, it seems, can produce mysteries as well as point toward their solutions.

–Richard A. Kerr

Additional Reading

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