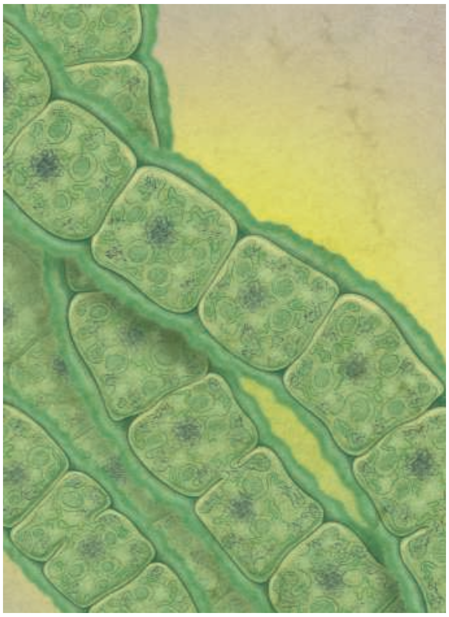
On the Origin of Photosynthesis



Try to picture the world without photosynthesis. Obviously, you'd have to strip away the greenery—not just the redwoods and sunflowers, but also the humble algae and the light-capturing bacteria that nourish many of the world's ecosystems. Gone, too, would be everything that depends on photosynthetic organisms, directly or indirectly, for sustenance—from leaf-munching beetles to meat-eating lions. Even corals, which play host to algal partners, would lose their main food source.

Photosynthesis makes Earth congenial for life in other ways, too. Early photosynthesizers pumped up atmospheric oxygen concentrations, making way for complex multicellular life, including us. And water-dwellers were able to colonize the land only because the oxygen helped create the ozone layer that shields against the sun's ultraviolet radiation. Oxygen-producing, or oxygenic, photosynthesis "was the last of the great inventions of microbial metabolism, and it changed the planetary environment forever," says geobiologist Paul Falkowski of Rutgers University in New Brunswick, New Jersey.

Given its importance in making and keeping Earth lush, photosynthesis ranks high on the top-10 list of evolutionary milestones. By delving into ancient rocks and poring over DNA sequences, researchers are now trying to piece together how and when organisms first began to harness light's energy. Although most modern photosynthesizers make oxygen from water, the earliest solar-powered bacteria relied on different ingredients, perhaps hydrogen sulfide. Over time, the photosynthetic machinery became more sophisticated, eventually leading to the green, well-oxygenated world that surrounds us today. In the lab, some biochemists are recapitulating the chemical steps that led to this increased complexity. Other researchers are locked in debates over just when this transition happened, 2.4 billion years ago or much earlier.

Looking so far into the past is difficult. The geological record for that time is skimpy and tricky to interpret. Eons of evolution have blurred the molecular vestiges of the early events that remain in living organisms. But "it's a terribly important problem," says biochemist Carl Bauer of Indiana University, Bloomington, one well worth the travails.

To catch a photon

Over more than 200 years, researchers have ironed out most of the molecular details of how organisms turn carbon dioxide and water into food. Chlorophyll pigment and about 100 other proteins team up to put light to work. Plants, some protists, and cyanobacteria embed their chlorophyll in two large protein clusters, photosystem I and photosystem II. And they need both systems to use water as an electron source. Light jump-starts an electrical circuit in which electrons flow from the photosystems through protein chains that make the energy-rich molecules ATP and NADPH. These molecules then power the synthesis of the sugars that organisms depend on to grow and multiply. Photosystem II—the strongest naturally occurring oxidant—regains its lost electrons by swiping them from water, generating oxygen as a waste product.

However, some bacteria don't rely on water as an electron source, using hydrogen sulfide or other alternatives. These nonconformists, which today live in habitats such as scalding hot springs, don't generate oxygen. Their photosynthetic proteins huddle in relatively simple "reaction centers" that may have been the predecessors of the two photosystems.

Envisioning the steps that led to this complex biochemistry is mind-boggling. Similarities between proteins in photosynthetic and nonphotosynthetic bacteria suggest that early microbes co-opted some photosynthesis genes from other metabolic pathways. But protophotosynthesizers might also have helped each other piece these pathways together by swapping genes. Biochemist Robert Blankenship of Washington University in St. Louis, Missouri, and colleagues say they've uncovered traces of these lateral gene transfers by comparing complete bacterial genomes. For example, their 2002 study of more than 60 photosynthetic and nonphotosynthetic bacteria (*Science*, 22 November 2002, p. 1616) suggested that bugs had passed around several photosynthesis genes, including some involved in synthesizing the bacterial version of chlorophyll.

Gene-sharing might also explain the puzzling distribution of the photosystems, Blankenship says. A cell needs both photosystems to carry out oxygenic photosynthesis. Yet modern nonoxygenic bacteria have the presumptive predecessor either of photosystem I or of photosystem II, never both. To explain how the two protein complexes wound up together, Blankenship favors "a large-scale lateral [gene] transfer" or even a fusion of organisms carrying each photosystem. However, other researchers remain skeptical, arguing that one photosystem evolved from the other, possibly through the duplication of genes, creating an ancient cell with both. No one knows for sure.

The electron thief

Either way, it took some fancy fiddling to convert the primitive reaction centers to oxygen-generating photosystems. Oxygenic photosynthesis was a huge upgrade, leading to a land of plenty, says biochemist John Allen of Queen Mary, University of London. "Water is everywhere, so the organisms never ran out of electrons. They were unstoppable."

But water clings to its electrons. With its oxidizing power, photosystem II can wrench them away, but the reaction centers in nonoxygenic photosynthesizers cannot. Biochemists James

THE YEAR OF

DARWIN

This essay is the third in a monthly series. More on evolution online at **blogs.sciencemag.org/origins**.

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Allen (no relation to John Allen) and JoAnn Williams of Arizona State University, Tempe, and colleagues are working out how a bacterial reaction center could have evolved photosystem II's appetite for electrons.

Taking a hands-on approach, they have been tinkering with the reaction center of the purple bacterium *Rhodobacter sphaeroides* to determine if they can make it more like photosystem II. First they targeted bacteriochlorophyll, the bacterial version of chlorophyll that's at the core of the reaction center, and altered the number of hydrogen bonds. Adding hydrogen bonds hiked the molecule's greed for electrons, they found.

The water-cleaving portion of photosystem II sports four manganese atoms that become oxidized, or lose electrons. So the team equipped the bacterial reaction center with one atom of the metal. In this modified version, the added manganese also underwent oxidation, the researchers reported in 2005. James Allen says that their creations aren't powerful enough to split water. But eventually, they hope to engineer a reaction center that can oxidize less possessive molecules, such as hydrogen peroxide, that would have been present on the early Earth. Even if the researchers never replicate photosystem II, "if we define the intermediate stages, we've accomplished a lot," he says.

Catching rays. Long before plants got in on the act, photosynthetic cyanobacteria living in pools like this one in Yellowstone National Park were changing the composition of the atmosphere.

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—Paul Falkowski, Rutgers University

Something in the air

How the photosystems got their start is crucial for understanding the origin of photosynthesis. But the question that's drawn the most attention—and provoked the most wrangling—is when photosynthesis began. Most researchers accept that nonoxygenic photosynthesis arose first, probably shortly after life originated more than 3.8 billion years ago. "Life needs an energy source, and the sun is the only ubiquitous and reliable energy source," says Blankenship.

The sharpest disputes revolve around when organisms shifted to oxygenic photosynthesis. At issue is how to interpret a watershed in the fossil record known as the great oxidation event (GOE). In rocks from about 2.4 billion years ago, geologists see the first unmistakable signs of significant, sustained levels of atmospheric oxygen. These signs include red beds, or layers tinged by oxidized iron, i.e., rust. Further support that the GOE marks an atmospheric revolution comes from a technique that detects skewed abundances of sulfur isotopes that occur if the air lacks oxygen. These imbalances persisted until the GOE, when they vanished.

Hard-liners construe these data to mean that oxygenic photosynthesis could not have emerged until shortly before the GOE. But other scientists disagree. "We are finding more and more hints that oxygenic photosynthesis goes deeper into the fossil record," says astrobiologist Roger Buick of the University of Washington, Seattle. These hints could push the origin back 600 million years or more.

One line of evidence is oil biomarkers that researchers think are the remains of cyanobacteria. They've turned up in rocks that are up to 2.7 billion years old. And in western Australia, thick shale deposits that are 3.2 billion years old hold rich bacterial remains but no traces of sulfur or other possible electron sources, suggesting that the microbes were using water to make energy.

Geologist Euan Nisbet of Royal Holloway, University of London, and colleagues found additional support for an early origin when they went searching for traces of RuBisCO, a key photosynthetic enzyme. RuBisCO feeds carbon dioxide into the reactions that yield sugars. The enzyme version found in oxygenic photosynthesizers plays favorites: It prefers carbon dioxide that contains the carbon-12 isotope over the bulkier carbon-13. In 2007, Nisbet and his colleagues found disproportionately low carbon-13 values indicative of RuBisCO activity when they analyzed organic matter in rocks from three sites in Zimbabwe and Canada that are between 2.7 billion and 2.9 billion years old. Nisbet concludes that oxygen-making photosynthesis began at least 2.9 billion years ago.

The early-origin case isn't ironclad. For example, a 2008 paper that has some researchers fuming claims that the oil biomarkers are contaminants that seeped in from younger rocks. Advocates also have to explain why it took hundreds of millions of years for oxygen to build up in the air.

Although the last word on the origins of oxygen-making photosynthesis isn't in, researchers say they are making progress. One thing is for certain, however: Without this innovation, Earth would look a lot like Mars.

–MITCH LESLIE