amino acid sequences of these receptors resemble that of p75, suggesting that p75 belongs to the same family.

Evidence that p75 can kill cells was quick to follow. In 1993, Dale Bredesen's group at the University of California, Los Angeles, reported that naked p75, unbound to NGF, kills cells, and that NGF blunts the killing. Although that was consistent with NGF's well-known role as cell savior, the idea that bare p75 kills ran counter to the behavior of other TNFR family members, which kill only when bound to their activating molecule, says Bredesen, now at the Burnham Institute in La Jolla, California.

Indeed, the idea of p75 as a killing molecule was not widely accepted. For example, in 1994 when Mark Bothwell's group at the University of Washington, Seattle, found that NGF binding to p75 causes cell death in a population of brain neurons, they did not interpret this as direct killing by p75. They proposed instead that NGF binding to p75 was preventing p75 from carrying out its auxiliary role of facilitating the binding of other neurotrophins to their Trk receptors, and as a result, the cells were losing a life-sustaining signal.

Barde, however, decided to test the possibility that NGF might directly instigate p75 to kill cells. He thought NGF might do this very early in development, a time when there is a lot of neuron death that has not been very well studied. Barde's team chose to study retinal neurons in very young chick embryos, which contain p75 but not TrkA. Normally, half of those neurons die in a programmed mass suicide that eliminates an excess of nerve cells during the fourth day of embryonic development.

But when Barde's group injected chick embryos with a monoclonal antibody to NGF that blocks its binding to p75, 80% of the neurons that would have died were saved. Further evidence of NGF's role in the neurons' death came when the Barde group found that the neurons could also be saved by antibodies that block NGF by binding to p75. "Early in development, cell death is triggered by the ligand [NGF] known to do the opposite later," Barde concludes.

Bredesen notes that because the retinal neurons Barde was studying, while lacking TrkA, still have Trk receptors for other neurotrophins, it's possible that NGF is acting indirectly, as Bothwell had hypothesized. And both Bothwell's and Barde's observations remain in inexplicable conflict with Bredesen's. "It is a hot field," says Bothwell, "but it is not really focused into a clear picture yet." As that picture begins to sharpen up, p75 and NGF are visible as central figures, even though exactly what they are doing remains a blur.

–Marcia Barinaga

STRUCTURAL BIOLOGY

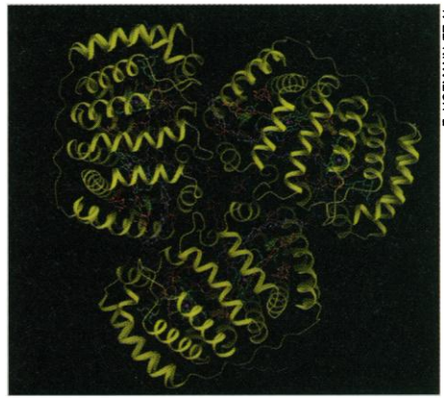
Form Follows Function When Plants Harvest Light

Anyone who has taken even an introductory biology class knows about the remarkable photosynthetic abilities of green plants. They can make complex organic molecules like sugars and starches from simple compounds like water and carbon dioxide, powered only by the energy they capture from sunlight. Far less well known, however, is a host of other photosynthetic organisms, including numerous bacteria and single-celled algae, such as the dinoflagellates that bloom periodically in poisonous "red tides." Obscure though they are, some of these organisms are masters of photosynthesis, harvesting wavelengths that green plants miss or converting light into stored energy with even greater efficiency. On page 1788, a team led by crystallographer Wolfram Welte of the University of Konstanz, Germany, and plant biologist Roger Hiller of Macquarie University in New South Wales, Australia, reports new findings that help explain why one of these organisms, the dinoflagellate *Amphidinium carterae*, is such an effective photosynthesizer.

From fluorescence studies, researchers already knew that the organism can capture light energy and transfer it with nearly 100% efficiency to the biochemical machinery that begins the job of converting it into chemical energy. Now, Welte, Hiller, and their colleagues have determined the structure, to a resolution of 2 angstroms, of one of *A. carterae*'s two light-harvesting "antennas." This is the peridinin-chlorophyll-protein (PCP), which is so called because the protein is associated with the pigments chlorophyll and peridinin, a type of carotenoid.

The structure shows that the peridinin and chlorophyll molecules are tightly packed within a vessel formed by the protein, an arrangement that allows for swift transfer of energy from the carotenoid, which captures the light, to the chlorophyll, which can then pass it on to the rest of the photosynthetic machinery. Says membrane biochemist Richard Cogdell of the University of Glasgow, Scotland, "It's a beautiful structure, aesthetically pleasing." Studies like this one, he notes, help explain why "there's a lot of interest in organisms that harvest light so well." Indeed, together with earlier structures of light-harvesting centers (LHCs) from other photosynthetic organisms, the results underscore the extent to which these complexes of molecules are tailored to each species' ecological niche.

It has, however, taken plant biochemists a full 20 years to begin to get an appreciation of the diversity of the LHCs, although chemical analyses provided some clues. Among other things, they showed that organisms in different environments may use different pigments, depending on the wavelength of light available. For example, *A. carterae*'s use of peridinin, which absorbs blue-green light, in the 470- to 550-nanometer range, is presumably an adaptation for collecting light in aquatic environments where light of that wavelength predominates. But a full understanding of how LHCs operate requires knowledge of how the pigments interact with each other and with the other components of the centers. And that information has been slow in coming, primarily because some structures are membrane-bound and difficult to isolate and prepare for crystallographic analysis using x-rays.



E. HOFMANN *ET AL.*

Light catcher. This *A. carterae* LHC contains three identical proteins (yellow-green), each with a cargo of chlorophyll (green), peridinin (red), and lipid (blue) molecules.

Indeed, the first two LHCs solved were not of the membrane-bound variety. In 1975, Brian Matthews of the University of Oregon, Eugene, and his colleagues obtained the structure of a soluble LHC, isolated from a species of green sulfur bacteria that lives at a depth of about 10 meters in lakes. And in 1985, Robert Huber and his colleagues at the Max Planck Institute in Munich, Germany, solved the x-ray structure of another soluble LHC, this one from the cyanobacterium *Mastigocladus laminosus*. These turned out to have distinctly different structures.

The sulfur bacterium's LHC, which absorbs blue light at about 460 nanometers

and in the near infrared, consists of three identical subunits, each containing seven chlorophylls enclosed within an envelope of protein. The cyanobacterium's LHC not only differed in the pigment used—phycobilins, which absorb in the 500- to 650-nanometer range (green, yellow, and orange light)—but in the LHC's shape, which consists of tiny rodlike assemblies.

The picture of LHC diversity has broadened over the past year and a half, as four new structures have come in, including the first of a membrane-bound LHC from a higher plant. As Werner Kühlbrandt of the European Molecular Biology Laboratory in Heidelberg, Germany, and his colleagues showed, this LHC, known as LHC II, consists of three identical proteins, each with three helices that are woven into the membrane of the chloroplast, the site of photosynthesis in higher plants. Associated with each protein are 12 chlorophylls and two carotenoids, which are also embedded in the membrane in close proximity to the helices and to each other.

Kühlbrandt notes that the arrangement of pigments and protein has apparently reached an optimal state because the LHC II proteins of higher plants have similar amino acid sequences, indicating that the structure has been conserved. "This structure is most successful at putting the maximum number of chlorophylls in the smallest space. It has the highest density of pigment per protein," Kühlbrandt says.

About 1 year ago, Cogdell's group at Glasgow and Simone Karrasch and her colleagues at the Medical Research Council (MRC) Laboratory in Cambridge, U.K., described both of the two sorts of membrane-bound LHC found in purple, nonsulfur, photosynthetic bacteria, which live almost everywhere. LH1 has one ring of chlorophylls plus protein, while LH2 contains two rings of chlorophyll molecules, one close to the membrane surface with the second set in the middle of the membrane bilayer. This arrangement, says Kühlbrandt, puts each ring of pigments in a different chemical environment, so "they absorb at different wavelengths, extending the spectral range of light harvested." That's a helpful adaptation for the bacteria, which often live in murky water, because it means they can use whatever light is available.

The latest LHC structure, from *A. carterae*, maintains the diversity trend. The Welte-Hiller team chose to study this LHC partly because it is rich in carotenoids, and none of the other LHCs whose structures are known use carotenoids as dominant pigments. The x-ray studies showed that this LHC consists of three identical proteins, whose structures are described by the researchers as resembling that of a ship in which the bow, sides, stern, and deck are formed by protein helices. Inside the hull of this ship is the cargo: two chlorophylls plus eight peridinin molecules plus two molecules of a lipid called digalactosyl diacyl glycerol. The lipid was a surprise because none have been documented in other LHCs. Welte and his Konstanz colleague Kay Diederichs speculate that the lipid might help keep the protein in its correct fold.

Johan Deisenhofer, of the University of Texas, Houston, adds that the elegant design of this LHC may also help to explain the superb success of PCP. He says that the shape of the hull puts the various pigments in extremely close proximity, only 3 or 4 angstroms apart, and oriented so that energy can easily be transferred from the peridinins to the chlorophylls. "It is interesting to see how nature solved the problem [of efficient light harvesting]," says Deisenhofer. "The geometry is key."

Researchers expect that they still haven't seen the full extent of the adaptations for light harvesting. "There will be an enormous array of these light-harvesting complexes," predicts structural biologist Richard Henderson of the MRC's Cambridge lab. "And each molecular structure will have its own knobs and whistles to improve the efficiency of light capture: It's a survival mechanism."

–Anne Simon Moffat

PHOTOVOLTAICS

New Solar Cells Seem to Have Power at the Right Price

Efficiency versus cost. It's a trade-off that bedevils makers of solar cells, frustrating their efforts to harness the sun. Cells made from wafers of crystalline silicon are rather good at absorbing photons and converting them to electricity. But they cost a lot to make. In contrast, noncrystalline cells made with an ultrathin film, amorphous silicon, are much cheaper. Their efficiency, however, is about half that of their crystalline counterparts. Now researchers think they can trade in this devilish trade-off.

New thin-film materials are showing signs that they can be both inexpensive and efficient, and have created "a sense of tremendous excitement in the technological side of the field," says Ken Zweibel, who heads thin-film solar cell research at the National Renewable Energy Laboratory (NREL) in Golden, Colorado. At a photovoltaic (PV) conference last month in Arlington, Virginia,* he and other participants were energized by a report that one material—a mixture of copper, indium, gallium, and selenium (CIGS)—has been made into prototype cells that convert nearly 18% of incoming sunlight to electricity, a performance approaching that of the best crystalline silicon cells. Hans Schock, a thin-film solar cell expert at the University of Stuttgart in Germany, says this result and others on display at the meeting "really give us a chance to bring the cost down."

How far down? Current crystalline solar cells can be built for manufacturing costs of $3.50 to $4 per watt generated. Many researchers expect the new thin films—CIGS and one other, a blend of cadmium and tellurium (CdTe)—to do better. If researchers can overcome nagging manufacturing and marketing problems, new devices could produce power for less than $0.50 per watt, low enough to make the cost of PV-generated electricity competitive with gas generators, says Zweibel. But those problems won't give way easily. CIGS, for instance, is difficult to deposit over large areas, and PV panels are window pane–sized; and anything made with cadmium, a toxic heavy metal, could face resistance from consumers.

To convert sunlight to electricity, all PVs rely on layers of semiconducting materials at their core. Electrons in these materials exist at discrete energy levels known as bands. When the material absorbs photons, the extra energy boosts electrons up to a higher "conduction" band, leaving behind positively charged "holes." Additional semiconductor layers above and below the absorbing layer then channel the electrons and holes in opposite directions, creating an electric current.

Conventional crystalline silicon PVs are good at this charged-particle steering, hence their efficiency. They are not so good at kicking electrons up to the conduction band; the photons need an extra energy boost from vibrations in the crystalline lattice, or phonons, to get the electrons to move. So solar-cell makers use large crystalline wafers up to 200 micrometers thick to give photons more opportunity to encounter phonons in the material. And the thickness of the material drives up the cost of the PVs.

* 25th IEEE Photovoltaic Specialists Conference, Arlington, VA, 13–17 May 1996.