

Photoreception

Bovine-like rhodopsin in algae

from Howard C. Berg

THE outer segment of the light-sensitive retinal rod has long been the system of choice for work on phototransduction in vision, from the isomerization of 11-*cis* retinal to the transient closure of sodium channels in the plasma membrane. Recent advances have centred on amplification involving GTP-GDP exchange, on activation of phosphodiesterase and on hydrolysis of cyclic GMP (Stryer, L. *Cold Spring Harb. Symp. quant. Biol.* **48**, 841; 1983). To those of us who work on sensory transduction in microorganisms, for example on chemotaxis in bacteria, it seems remarkable that so much has been learned without the use of genetics. There is nothing like the right mutant to open the door to fresh discovery, to reveal an unsuspected component or process essential to the function of a complex biological machine. The report on page 756 of this issue that the green alga *Chlamydomonas* can see with the aid of a bovine-like rhodopsin foreshadows a renaissance in studies of eukaryotic photoreception.

Chlamydomonas is an aquatic organism about 10 μm in diameter that is propelled along a helical path by means of two anterior flagella. For photosynthesis, the cell uses blue and red light, which it detects using one chloroplast while for phototaxis, it uses blue-green light, which it detects with one lateral eye, or eyespot. It swims towards or away from a source of light, aligning the axis of its helical path with that of the beam. In 1980, Foster and Smyth argued that the eyespot is a directional antenna, comprising alternate layers of material of different refractive index, that enhances contrast on a layer of photoreceptor pigment in the overlying plasma membrane (*Microbiol. Rev.* **44**, 572). They noted that this antenna completes a 360° lateral scan of the environment every time the cell advances one helical turn. Using a phase-sensitive system that causes one flagellum to pull harder than the other when the output of this scan is non-uniform, the cell can correct its course and 'lock on to' the beam. On the basis of the phototactic action spectrum and other optical properties of the cell, they predicted that the photopigment would be a bovine-like rhodopsin.

Now Foster and his associates, using retinal analogues provided by Nakanishi's group, have proved the point. Phototaxis of a carotenoid-free mutant is restored on addition of suitable analogues, and the shifts in the action spectra parallel those seen in absorption spectra of bovine rhodopsins. The pigment protein clearly differs from bacteriorhodopsin, which works with different analogues and has

different spectral properties.

Most steps of the sensory pathway remain to be worked out. Coupling to the flagella presumably occurs via changes in membrane potential, since such changes are observed, with the appropriate action spectrum, when a related green alga, *Haematococcus*, is exposed to light (Litvin, F.F., Sineshchekov, O.A. & Sineshchekov, V.A. *Nature* **271**, 476; 1978). The two flagella of *Chlamydomonas* have different sensitivities to calcium ions (Kamiya, R. & Witman, G. B. *J. Cell Biol.*

98, 97; 1984), so voltage-sensitive calcium channels might be involved. Little is known about how light absorption generates changes in membrane potential. It is at the level of these early steps in phototransduction that we can expect to see the most significant advances.

Lest anyone should doubt the power of genetic and biochemical dissection in *Chlamydomonas*, look how it has broadened our understanding of the assembly, structure and function of the eukaryotic flagellum (Luck, D.J.L. *J. Cell Biol.* **98**, 789; 1984). Similar breakthroughs should now be possible in studies of eukaryotic photoreception. □

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Palynology

Andean guide to Pliocene-Quaternary climate

from J.R. Flenley

THE city of Bogota, 2,600 m up in the Colombian Andes, enjoys a remarkably level site, being built on the dry bed of a former lake. A resistivity survey has recently shown that the lake deposits are 800 m deep and have probably been accumulating continuously from well back in the Pliocene and throughout the Quaternary. This has provided a unique opportunity to obtain a complete land-based record of the climatic oscillations of the Quaternary to complement the existing deep-sea record. The results are contained in *Vegetational and Climatic History of the High Plain of Bogota, Colombia: a Continuous Record of the Last 3.5 Million Years* (Cramer, Liechtenstein; 1984), by H. Hooghiemstra.

The deep-sea record has been investigated by Nick Shackleton from Cambridge, and Neil Opdyke at Lamont-Doherty Geological Observatory. By oxygen isotope analysis of the shells of foraminifera from the ocean-bed ooze they have shown that there were numerous major climatic cycles in the past 1.6 Myr, that is since the Olduvai magnetic event which provides one possible definition of the Pliocene-Quaternary boundary. Oxygen isotopes, however, though giving an indication of the amount of ice in the world and of the palaeotemperature of the ocean surface, tell one little about ecological conditions on the continents. In that respect the continuous land-based record from Bogota is very important indeed.

The Bogota sediments have now been cored to a depth of 357 m. Fortunately they contain numerous bands of volcanic ash, which can be dated by the potassium-argon method, allowing it to be established

that this part of the record covers the last 3.5 Myr. The monumental task of pollen-analysing this core fell to Henry Hooghiemstra and O.K. Hulshof, working with Tom van der Hammen at the Hugo de Vries Laboratorium in Amsterdam. After 1,230 pollen samples and 378 pollen and spore types, they graphed their results with a laser-beam plotter.

The resulting diagram has been divided into no less than 55 zones, representing 27 complete major climatic cycles, which can be correlated with those from the deep-sea record, and extend it much further back in time. The fluctuations in mean annual temperature are from <6°C to >15°C — so much for those who would write off Quaternary temperature change in the tropics. Some of the most marked fluctuations and some of the coolest temperatures occur in the Pliocene part of the record. It seems that the Late Tertiary was not the time of gently declining temperatures which it was once thought to be.

The great advantage of a land-based core over an ocean core is that it gives direct biogeographical and ecological information. The Isthmus of Panama and the Andes were formed relatively late in the Tertiary, before which it was almost impossible for taxa from North America to migrate into South America. In the Bogota record, we can actually see the arrival of the North American trees *Quercus* and *Alnus*. *Alnus* arrived in the Late Pliocene, about 2.9 Myr ago; *Quercus* appeared on the scene only 1.0 Myr ago. Such direct evidence of migration provides a factual basis for biogeography and offers essential tests for the hypotheses put forward by students of modern biogeographical distributions.