to have stumbled accidentally across these tar pools, but we suggest that some animals were deceived by and attracted to the pits by the strong reflection–polarization of the oil surface mimicking a body of water.

Gábor Horváth*
Biophysics Group,
Department of Atomic Physics,
Lorand Eotvos University,
H-1088 Budapest, Puskin u. 5-7, Hungary
Jochen Zeil*
Kuwait University, Faculty of Science,
Department of Zoology, PO Box 5969,
SAFAT, 13060 Kuwait

*Present addresses: Lehrstuhl für Biokybernetik, Universität Tübingen, Auf der Morgenstelle 28, D-72076 Tübingen, Germany (G.H.); Centre for Visual Sciences, RSBS, Australian National University, PO Box 475, Canberra, ACT 2601, Australia (J.Z.).

Hidden quasars reddened by dust?

SIR — Webster *et al.*[1] argue for a large population of dust-reddened quasars, on the basis of the optical–infrared colour diversity in their new sample of radio-loud quasars with flat radio spectra. If their sample is representative of the quasar population, then their results imply that optical surveys miss about 80% of quasars, and that these missing quasars could account for the observed X-ray background. We argue that there is a simple way of avoiding these radical conclusions. Their results are influenced by an additional red, optical synchrotron component peculiar to flat-spectrum radio-loud quasars, with its own resulting colour diversity caused by the range in relative contributions of the 'normal' quasar and synchrotron components.

Flat radio spectra in quasars are caused by enhancement of synchrotron emission from compact regions within a jet by relativistic beaming in the direction of its motion[2]. Selecting by flat radio spectral index should therefore bias strongly in favour of quasars whose radio jets lie very close to the line of sight. In the context of Unified Schemes[2] in which the jet emerges along the relatively unobscured poles of an anisotropic distribution of material, or in which the jet itself clears material along its path, flat-spectrum quasars should be subject to very little intrinsic reddening .

It has been known for many years, however, that flat-spectrum quasars can have unusually red optical–infrared colours (for example, ref. 3). In several cases there is direct evidence from time variability that these colours are the result of a non-thermal source of red light which is superimposed on the normal blue quasar continuum (for example, ref. 4) and which is likely to be an extension of the synchrotron emission that dominates in the radio; many other studies also suggest the presence of a beamed optical–infrared component (for example, ref. 5). Indeed, many of the Webster *et al.* quasars are classified optically as blue stellar objects, despite their red optical–infrared colours[6]. This argues strongly against a reddening interpretation, but is consistent with a beamed, red synchrotron component.

Such a beamed component of optical emission may also explain the unusually large range of broad-line equivalent widths amongst flat-spectrum quasars (compare ref. 7 with Webster *et al.*'s Fig. 2; see also ref. 5). An observable anti-correlation of broad-line equivalent widths with *B–K* colour is not a firm prediction of the beaming model because the combined dispersion in the equivalent widths, the unbeamed continuum slope, and the slope of the (variable) beamed component may be very large. However, Jackson *et al.*[8] have demonstrated an anti-correlation between the dominance of flat-spectrum radio emission and the equivalent widths of the emission lines. This is strong evidence for an additional source of continuum emission in flat-spectrum quasars which, if red (as expected for synchrotron emission), provides a simple explanation for the colour diversity reported by Webster *et al.*

Some quasars may be reddened by the mechanism favoured by Webster *et al.* The well-known population of red quasars associated with steep-spectrum radio sources, in which the red beamed optical component is not expected to dominate, have broad lines sometimes only revealed by near-infrared spectroscopy[9]. Nevertheless, complete surveys at low radio frequencies[10], which are insensitive to beamed objects, contain few red quasars, again suggesting that the incompleteness in optical quasar surveys is much less dramatic than concluded by Webster *et al.*

Perhaps a more pertinent question is whether narrow-line objects constitute a population of obscured quasars. Studies of steep-spectrum radio sources[2] are consistent with the hypothesis that narrow-line radiogalaxies are quasars whose nuclei are obscured by material with column densities orders of magnitude higher than those invoked by Webster *et al.*

Stephen Serjeant
Astrophysics Group,
Blackett Laboratory,
Imperial College, London SW7 2BZ, UK
Steve Rawlings
Department of Astrophysics,
Nuclear Physics Laboratory,
Oxford OXI 3RH, UK

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New photosynthesis or old?

SIR — Greenbaum *et al.*[1] have described the light-induced hydrogen and oxygen evolution in a mutant strain of the green alga *Chlamydomonas reinhardtii* lacking photosystem I (PSI). As the mutant cells consumed carbon dioxide in the light, Greenbaum *et al.* suggested that reduced NADPH (nicotinamide adenine dinucleotide phosphate, obligatory for carbon fixation and normally formed by PSI) was generated by the direct reduction of $NADP^+$ by pheophytin, the low-potential electron acceptor of photosystem II (PSII)[2]. The authors claimed "a new type of photosynthesis being performed by the PSII light reactions exclusively".

Transient photosynthesis has been reported from a *Chlamydomonas* mutant lacking PSI (for example, ref. 3), as has direct reduction of $NADP^+$ by pheophytin in various PSII-enriched preparations (for example, refs 4, 5). The quantum yields were low in the latter case[6]. Apparently, the forward electron transfer from the reduced pheophytin to $NADP^+$ was not competitive with its backreaction (occurring in a few nanoseconds[7]) with the oxidized primary electron donor of PSII. The experiments with the PSI-lacking mutants, however, yielded a high rate of carbon dioxide consumption, comparable to that in wild-type cells. This high quantum yield may point to another mechanism of $NADP^+$ reduction.

The photosynthetic reaction centre of purple photosynthetic bacteria is evolutionarily and functionally related to PSII[8] (except for its inability to oxidize water). Bacteriopheophytin, with the same low redox potential as its counterpart in PSII[9], does not directly reduce nicotinamide dinucleotides. Instead, they are formed by reversed electron flow through the NADH:ubiquinone oxidoreductase complex. The driving force of the reversal consists of the scalar reducing potential of the ubiquinone/ubiquinol redox pair plus the electrochemical potential difference of the proton across the photosynthetic membrane[10]. *Chlamydomonas reinhardtii* incorporates an active NAD(P)H:plastoquinone oxidoreductase in its thylakoid membrane[11,12]. Thus, we propose a more traditional interpretation of the data by Greenbaum *et al.*, namely, that electrons provided by PSII first reduce the plasto-

quinone pool and only then does the protonmotive force drive them into $NADP^+$. Both conflicting hypotheses can be discriminated by applying uncouplers and plastoquinone antagonists. Until the necessary tests have been performed, the question of an efficient, physiologically relevant, direct reduction of $NADP^+$ by PSII, and hence the challenge to the general validity of the Z-scheme of Hill and Bendall[13], remains unsettled.

Armen Y. Mulkidjanian, Wolfgang Junge
Division of Biophysics,
Faculty of Biology/Chemistry,
University of Osnabrück,
D-49069 Osnabrück, Germany

GREENBAUM *ET AL.* REPLY — In our Letter we reported a new phenomenon, CO_2 fixation and hydrogen and oxygen evolution, at wild-type rates, in a mutant alga that lacked the photosystem I reaction centre. We did not, however, attempt to elucidate the mechanism or the pathway of this discovery, or claim evidence for "the direct reduction of $NADP^+$ by pheophytin..."

Mulkidjanian and Junge speculate that the mechanism of 'PSII photosynthesis' is reversed electron flow through the NAD(P)H:plastoquinone (PQ) oxidoreductase in the thylakoid membrane, as previously advanced by Peltier and Thibault[14] to explain electron transport in isotopic oxygen exchange experiments in F18, another PSI-deficient mutant of *Chlamydomonas reinhardtii*. We considered this mechanism, but we are convinced that this explanation is not correct. Antimycin A is known to inhibit chlororespiration by blocking electron transport between NAD(P)H and the PQ pool which is mediated by the thylakoid membrane-bound NAD(P)H–PQ oxidoreductase[15,16]. Our recent experiments (J.W.L. and E.G., manuscript in preparation) indicate that antimycin A has no effect on PSII photosynthesis.

In addition, we have found that 5 μM FCCP (carbonyl cyanide trifluoromethoxyphenyl hydrazone) completely inhibits CO_2 photoassimilation but increases the sustained simultaneous photoevolution of molecular hydrogen and oxygen. FCCP is a protonophore that dissipates proton gradients across the photosynthetic membrane and thus inhibits synthesis of ATP, which is essential for CO_2 assimilation by the Calvin cycle but not essential for hydrogen production by the ferredoxin/hydrogenase pathway. It is known that the reverse-operating NAD(P)H:PQ oxidoreductase is driven by a proton gradient across the thylakoid membrane. If such a reverse-operated mechanism were responsible for electron transfer from PQH_2 to ferredoxin, FCCP would inhibit not only CO_2 assimilation but also H_2 photoevolution, because both are dependent on electron transfer from PQH_2 to ferredoxin. FCCP's effect cannot be explained by the reverse-operating NAD(P)H:PQ oxidoreductase mechanism.

Moreover, we have demonstrated that PSI-deficient green algae can grow photoautotrophically using CO_2 as the sole source of carbon, light as the sole source of energy, and water as the sole source of electrons under both aerobic and anaerobic conditions in a minimal medium (water plus mineral elements but without organic nutrients; J.W.L., C.V.T., L.J.M., T.G.O. and E.G., manuscript submitted). Photoautotrophic growth and the quantum requirement of photosynthesis in PSI-deficient mutants (E.G., J.W.L. and C.V.T., manuscript in preparation) preclude the reverse-operating NAD(P)H:PQ oxidoreductase from being responsible for PSII photosynthesis.

Mulkidjanian and Junge state that their proposed mechanism uses the scalar reducing potential of the ubiquinone/ubiquinol redox pair plus the electrochemical proton potential difference to drive the reduction of $NADP^+$. Even if the operation of that mechanism can generate NADPH, it will leave little or no proton-gradient energy for synthesis of ATP, which is required for CO_2 fixation by the Calvin cycle as well as for cell growth. This mechanism cannot, therefore, explain our newly discovered PSII photosynthesis and its support of photoautotrophic growth. We believe that the mechanism of PSII photosynthesis involves electron flow from PSII to ferredoxin/$NADP^+$ reduction through the plastoquinone pool and cytochrome *b/f* complex (J.W.L. and E.G., manuscript in preparation).

E. Greenbaum, J. W. Lee
C. V. Tevault, S. L. Blankinship
Chemical Technology Division,
Oak Ridge National Laboratory,
Oak Ridge, Tennessee 37831, USA
L. J. Mets
Department of Molecular Genetics and Cell Biology,
University of Chicago,
Chicago, Illinois 60637, USA

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Lateral proton diffusion

Sir — The lateral diffusion of protons along membranes could provide a direct link between sources and sinks involved in chemiosmotic coupling[1]. Recently, a long-distance migration of protons along membranes has been observed in purple membranes and reconstituted bacteriorhodopsin[2–5]. This was suggested to be due either to protonation/deprotonation reactions of amino groups or polar headgroups of lipids, or to a movement along interfacial water molecules[2–5]. Scherrer has suggested that evidence for a lateral movement of protons along a surface could be obtained by modulation of the chemical character of the lipid headgroups[5]. The dwell time of protons depends on the lipid headgroups[6], and so this is expected to control any lateral proton movement. Studies on dissociation rate constants concluded that surface-to-bulk proton transfer was not retarded and so there was no lateral proton movement[7,8].

The experiments proposed by Scherrer have already been performed in lipid monolayers, by comparing long-range movements of protons from a source to detectors either at the membrane level or in the bulk medium (as reviewed in ref. 9). Lateral migration of protons is observed with many phospholipids as long as the molecular assembly is in the fluid state, and is therefore not controlled by the chemical character of the polar heads. Rather, the migration of protons along membranes may be supported by a hydrogen-bond network involving polar headgroups and interfacial water molecules. A 'hop and turn' mechanism would be involved and controlled by the correlation time of the lipid headgroups, as experimentally observed, and not their chemical character. As soon as the continuity of the network is broken (for physical or chemical reasons), the lateral migration of protons is prevented.

Migration was critically controlled by the composition of lipid/detergent mixed

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