

species, physiologies and ecologies, and adding further pieces to the puzzles of global biogeography and evolution of vent faunas. We know that vent faunas are regionally disparate; each sampling of remote sites yields dozens to hundreds of new species, and insight into their distribution and evolution.

Equally exciting is the fact that German and colleagues' findings mean that nowhere is sacred. We can expect to find hydrothermal vents in extremely isolated ridge segments, despite their slow spreading rates. High on the wish-list of vent biogeographers is access to a vent site on the Cayman rise in the Caribbean, where the spreading rate is even slower than on the southwest Indian ridge. Will the fauna of a Cayman vent be Atlantic or Pacific in nature? Or will it be more closely related to seep faunas of the Gulf of Mexico? What of the fauna of slow-spreading Arctic ridge hydrothermal vents, which are located in a basin where the deep water has long been isolated from the major oceans? And what of the putative vent fauna of the Scotia ridge, that island of a spreading

centre that lies well west of the southern Mid-Atlantic Ridge?

It is to these remote ridge systems that I look for vindication of what I think of as the 'trilobite factor' — the belief that there are still major discoveries waiting for us in unexplored regions of the ocean. Trilobites, of course, have been extinct since the Permian, some 250 million years ago, and the chances of finding some deep-water relative of these fossil arthropods teeming about an abyssal hot spring are perhaps remote to nil. But, if not trilobites, surely other unimagined celebrations of nature's ingenuity will be found. □

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Protein transport

The doors to organelles

Gottfried Schatz

Mitochondria import most of their proteins from the surrounding cytosol. During this process, proteins destined for import are first selected from the thousands of cytosolic proteins and are then transported into or across the outer membrane of the organelle. Finally, many of them must be sorted to their correct destination inside. Reports by Hill *et al.*¹ (page 516 of this issue) and Künkele *et al.*² (in *Cell*) now provide exciting information on the molecular architecture of the channels that transport proteins through the outer membranes of mitochondria.

The protein-transport channel in the yeast mitochondrial outer membrane was first identified by crosslinking one of its subunits to an artificial precursor protein stuck in the channel³. The subunit, now termed Tom40 (ref. 4), is an integral membrane protein (relative molecular mass, M_r , 40,000) that is essential for viability of yeast cells. Tom40 is part of a large 'Tom complex' (Fig. 1) that also contains the small, membrane-embedded subunits Tom5, Tom6 and Tom7, as well as subunits with cytosolically exposed domains (Tom20, Tom22, Tom37 and Tom70). Tom40 is buried in the mitochondrial outer membrane, which it seems to span almost exclusively in the form of β -strands⁵. This topology resembles that of the pores in bacterial outer membranes, so Tom40 was suspected to form the core of the protein-transport channel.

Hill *et al.*¹ now provide direct and convincing evidence for this hypothesis. They overproduced yeast mitochondrial Tom40 in *Escherichia coli* and purified it by denaturation followed by renaturation. They then incorporated the pure Tom40 asymmetrically into liposomes or planar phospholipid bilayers, and showed that the reconstituted protein forms a hydrophilic, cation-selective transmembrane channel. The channel is partly blocked by a peptide representing a functional mitochondrial targeting sequence, but only if the peptide is added to the side of the artificial membrane that corresponds to the cytosolic face of the mito-

chondrial outer membrane. Calculations based on the channel conductance indicate a pore diameter of 12 to 26 Å, depending on the assumed resistivity on the channel — when the authors calibrated the channel with differently sized cations they found a pore diameter of 22 Å. This value agrees with observations that the channel is big enough to allow the passage of precursors that are attached to double-stranded DNA⁶. Furthermore, measurements of the Tom channel with calibrated gold particles yield a value of greater than 22 Å but less than 26 Å (A. Matouschek, personal communication).

What does the protein-import machinery look like in the mitochondrial outer membrane? In a remarkable *tour de force*, Künkele *et al.*² have purified the whole Tom complex from mitochondria of the fungus *Neurospora crassa*, determined its subunit stoichiometry, and verified its functional integrity by reconstitution experiments similar to those reported by Hill and colleagues. Künkele *et al.* also examined the morphology of the channel by negative staining and high-resolution electron microscopy. The filtered images reveal particles with one, two or three stain-filled holes. The 20-Å diameter of the holes agrees reasonably well with the ion conductance of the reconstituted complex if some additional assumptions are made. If each stain-filled hole were indeed a protein channel, an intact Tom complex would have three protein channels.

Whereas subunits of the protein-transport system in mitochondria are called Tom, in chloroplasts they are known as Toc (ref. 7), although no Toc subunit shows any sequence similarity to any Tom subunit. Proteins enter chloroplasts through the Toc complex in the outer membrane (Fig. 1). Toc86 (which is now thought to be a proteolytic fragment of a protein, M_r 159,000, and should be renamed Toc159; D. Schell, personal communication) and Toc34 seem to be GTP-regulated import receptors; the function of Toc36 is still under debate; and Toc75 is thought to form the protein-

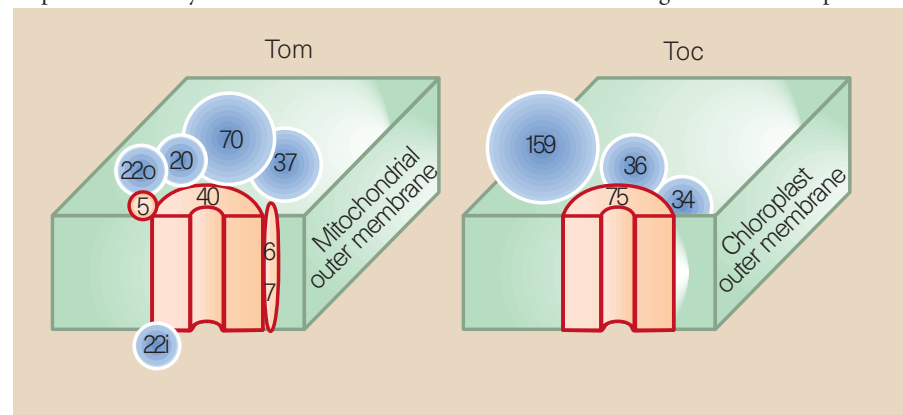


Figure 1 The protein-transport channels in the outer membrane of mitochondria (Tom) and chloroplasts (Toc). Tom22 has extra-membrane domains (Tom22o and Tom22i) on both sides of the outer membrane. The role of Toc36 is still uncertain. The drawing does not indicate the number of each subunit per complex.

transport channel because it is almost completely embedded in the membrane, and is predicted to span the outer membrane through 16 β -strands⁸. In a seminal study, Hinnah *et al.*⁹ incorporated recombinantly expressed and purified Toc75 into liposomes or planar phospholipid bilayers and found that the protein formed voltage-dependent ion channels with weak cation selectivity. The channel was partly blocked by a chloroplast precursor protein, but not by the corresponding mature protein. As in Hill and colleagues' study, the precursor protein inhibited the channel only if it was added to the side of the membrane corresponding to the cytosolic face of the chloroplast outer membrane. The conductance of the Toc75 channel suggested a pore diameter of only 8 Å, but this was not corrected for possible channel resistivity and is probably a minimal value. So despite their different primary sequences, Toc75 and Tom40 have a similar transmembrane topology and function.

The protein-transport channels across another organelle, the endoplasmic reticulum, open only in response to an appropriate precursor protein — they are gated¹⁰. Gating must also be inferred for the corresponding channels across the proton-impermeable inner membranes of mitochondria, chloroplasts and Gram-negative bacteria.

Although there is no direct evidence that protein channels in the outer membranes of mitochondria and chloroplasts are gated, Hill *et al.*¹ find that the Tom40 channel has a three- to fourfold lower probability of opening if it is reconstituted from total outer membranes instead of from purified Tom40. Gating may be effected by the small Tom subunits, which have already been shown to modulate the flexibility of the Tom channel¹¹. In sum, we know the door through which proteins enter mitochondria and chloroplasts, but must still find the parts that make it a gate. □

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Active galaxies

Light jets near light speed

Tom Jones

What creates the high-speed jets of material that emerge from quasars, radio galaxies and other active galactic nuclei? On page 457 of this issue¹, Wardle *et al.* report the detection of a subtle but telling feature in the radio emission from the inner jet of the violently variable quasar 3C279. They present the first reliable images and spectral distributions of circularly polarized emission from such a jet — the strongest evidence yet that these jets are mostly made of electron–positron pairs, many at low energies. Similar reports by these observers are available² for three other galaxies, 3C273 (Fig. 1), PKS0530+134 and 3C84. So what does that tell us about the processes that accelerate these jets, presumably in the innermost regions of active galaxies?

Any galaxy whose central emission does not appear to be coming from stars is said to have an active galactic nucleus (AGN). AGNs often emit radiation at a very wide range of wavelengths, from radio waves to γ -rays, and some of them are the most luminous objects in the Universe. Although they are diverse in their spectrum and luminosity, we can explain most of their properties using a single, fairly simple theoretical picture. But this picture has two superficially

contradictory central elements.

We believe that in all these objects, gas falls onto a very massive black hole in the galactic nucleus³ — sometimes called the 'beast'. Because it has some angular momentum, the gas forms an accretion disk^{4,5}. Friction dissipates the angular momentum, allowing the gas to move inwards and heating it up, and thermal emission from this hot gas is thought to be responsible for most of the energy released by a typical AGN,

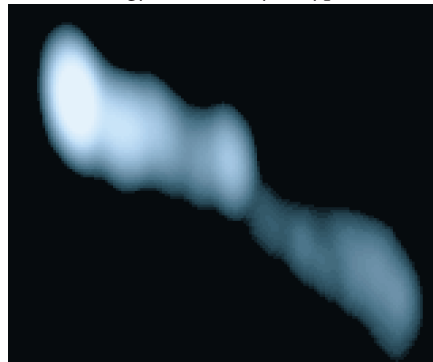


Figure 1 A jet in the quasar 3C273. Its inner few hundred parsecs show up here in 15-GHz radio waves. It is probably an electron–positron plasma, travelling away from a central supermassive black hole at nearly the speed of light.

especially between the infrared and X-ray bands. That much of the picture is fairly clear, both observationally and theoretically. We even find similar accretion disks in other compact astronomical objects, such as newborn stars surrounded by remnants of their birth, and white dwarfs and neutron stars collecting mass from close binary companions, so AGN disks are only the most extreme cases of a common natural phenomenon.

That brings us back to jets, the second element of the AGN picture. Given that AGNs are powered by infall, it is perhaps strange that many have very fast outflows, in the form of highly collimated jets of plasma. These jets are believed to be produced by an interaction between the accretion disk and the central black hole³, in a region so small that it may be impossible to observe directly. So jet properties reflect conditions in a crucial region that is otherwise very difficult to probe.

Since the first jet-like structure was recognized in the relatively nearby galaxy M87 in the 1950s, jets have been studied in many electromagnetic wavebands, and especially in radio waves. Astronomers have discovered that the giant lobes of radio emission seen on either side of some AGNs are connected to the parent galaxy and its nucleus by jets that are sometimes hundreds of kiloparsecs long. Even more dramatically, they have found evidence for rapid expansion along the first few parsecs of some jets⁶, at up to ten or more times the speed of light. At first these 'superluminal motions' caused quite a flurry, because they appear to violate relativity, but it was soon accepted that the apparent superluminal motion is a relativistic illusion that results when the jet is tilted slightly away from the line of sight, and the speed is close to the speed of light (perhaps just a fraction of a per cent less). Within the past few years, similar discoveries have been made for stellar-mass X-ray objects within the Milky Way⁷. So how are jets accelerated to almost the speed of light?

One of the keys to unravelling the origin of jets is to establish their composition. The radio emission is almost certainly synchrotron radiation coming from highly relativistic electrons in a magnetic field. But what balances the electrons' negative charge? Is it protons or positrons? Enter Wardle *et al.*¹. They have managed to detect and image circularly polarized radio emission coming from the parsec-scale jet in 3C279. The observations are an impressive feat, as this polarized signal is very weak and a number of pitfalls must be avoided. Their reward is a clear, direct look at the mass and energy composition of the plasma in the radio jet.

In general terms, polarization depends on the symmetries of the environment where radiation is generated, and through which it passes. To a first approximation, synchrotron emission is plane polarized perpendicular to