LSGGQ motif of BtuD is pulled away from the Walker A motif of the opposing subunit by about 4 Å relative to the same motif in the Rad50 structure, where residues from both motifs make contact with bound ATP (*9*). Thus, activation of ATP hydrolysis may be associated with movement of the LSGGQ motif into contact with the phosphates of ATP (*11*). Likewise, release of ADP and/or $P_i$ (inorganic phosphate) following hydrolysis may require the withdrawal of the LSGGQ motif (*10*). Because the two ATP-binding cassettes are tightly associated with the two transmembrane subunits, one can imagine that movement of the two cassettes relative to each other in response to ATP binding and hydrolysis could translate into movements that open the gate between the two transmembrane subunits, allowing $B_{12}$ to enter the cytoplasm through the central channel (see the bottom figure).

This picture, however, is only partially complete. What prevents $B_{12}$ from escaping back into the periplasm (leading to ATP hydrolysis without $B_{12}$ transport)? Enter the periplasmic binding protein. Chen *et al.* (*12*) have recently shown that the periplasmic maltose binding protein is required for coupling maltose transport to ATP hydrolysis. In addition to binding the substrate with high affinity, the binding protein also stimulates ATP hydrolysis, becoming tightly bound to the transporter in the catalytic transition state, when ATP is trapped between the two subunits. Taking a cue from the maltose transport system (*12*), the tight binding interactions in the Btu system that are expected to develop during ATP hydrolysis—between the binding protein (BtuF) and the BtuC subunits, and between the BtuD subunits and ATP molecules along the dimer interface—may reduce the affinity of the binding protein for $B_{12}$ as the gate opens to the cytoplasm. These simultaneous changes will allow $B_{12}$ to dissociate and enter the cytoplasm, but not the periplasm, which is temporarily blocked by the physical presence of the binding protein BtuF in the transporter complex (see the bottom figure).

The BtuCD structure has a vestibule between the four subunits that appears large enough to allow release of $B_{12}$ into the cytoplasm even while the ABC subunits are tightly engaged. A complex of transporter and binding protein resembling the catalytic transition state can be stabilized with phosphate analogs such as vanadate (*12*) or aluminum fluoride. Comparison of the ground state, as seen in the Locher *et al.* structure, with an intermediate resembling the catalytic transition state should elucidate the conformational changes that couple transport to ATP hydrolysis in an ABC transporter. Finally, the structural diversity of the transmembrane region documented by the first two structures of complete ABC transporters, each of which is tailored to do a specific job, underscores the importance of performing these experiments in many different ABC transporters to obtain a full understanding of how the energy of ATP hydrolysis can be harnessed to do work.

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PERSPECTIVES: RADIO GALAXIES

# Bubbles, Flows, and Fields

**A. C. Fabian**

Most galaxies, including our own, appear to have a massive black hole at their center. Some, the active galactic nuclei, are visible to us as a result of luminous outpourings such as quasars and the less powerful Seyfert galaxies. About 10% of active galactic nuclei are strong radio emitters. Diametrically opposed pairs of powerful energetic jets squirt out of these "radio-loud" objects at relativistic speeds. The jets themselves are rarely detected; the strongest evidence for their existence may be a pair of lobes of radio-emitting material on either side of the nucleus where the jets are shocked and decelerated by surrounding gas.

The first of these jets was sighted by H. Curtis almost 90 years ago in the giant elliptical galaxy M87 in the Virgo cluster. Twin radio lobes were reported almost 50 years ago. Yet the matter content of jets (apart from the emitting electrons), their total power, and their evolution remain uncertain. The high spatial resolution x-ray imaging achieved by NASA's Chandra observatory is, however, beginning to answer these questions.

X-ray observations have proven so useful because the gaseous atmospheres that fuel the jets usually have temperatures on the order of $10^6$ to $10^7$ K. By studying the surrounding gas, particularly bubbles in the gas blown by the jets, their total power and history over the past $10^7$ to $10^8$ years can be deduced. Holes and depressions in the x-ray emission have now been seen around radio sources in numerous clusters, including the Virgo cluster, the Perseus cluster, Hydra A, and the Centaurus cluster (*1–5*).

The relativistic jets are believed to originate very close to the central black hole and are probably ejected up the rotation axis of the accreting gas, or the spin axis of the black hole itself. As the jet decelerates in the surrounding matter, a bubble of low-density heated gas and relativistic plasma accumulates about the end of the jet. Unless the jet is so powerful that it dominates the hot gas, the bubble expands until buoyancy forces cause it to rise up and break away as a new bubble forms. The situation is similar to that of a dripping tap, with relative densities and directions reversed.

A bubble appears as an x-ray hole because its density is low. Provided that the bubble is not expanding supersonically (which is unlikely because the x-ray images show no evidence for shocks), its pressure should be similar to that of the surrounding gas, which can be deduced from the x-ray data. Pressure is proportional to energy density, and the volume of the bubble therefore gives an estimate of its total energy. The age of the bubble can be derived from the buoyancy force, yielding the mean total power of the jets.

Alternatively, these quantities can be deduced from only the radio data. The pressure can be deduced, assuming that the total energy of the cosmic rays and magnetic field that produce the synchrotron radio emission is minimized. The age can be deduced by identifying a spectral break in the power-law spectrum due to synchrotron losses. The energy may not be at a minimum, however. Furthermore, the pressure associated with the positively charged particles presumed to accompany the radiating electrons has to be accounted for, as well as any other relativistic components that do not contribute to the observed waveband.

With standard parameters, this method

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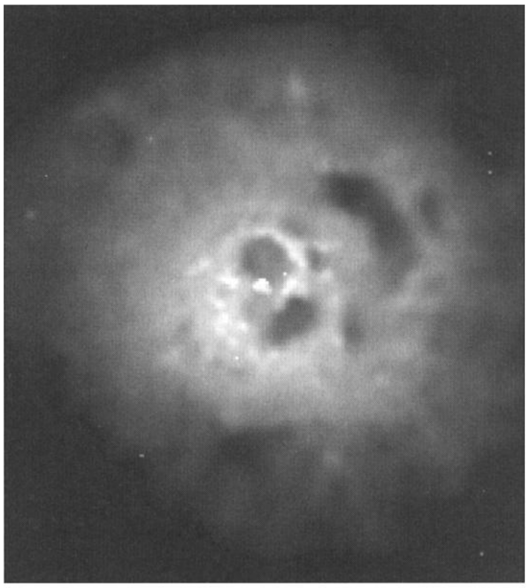
yields a much lower pressure for the bubbles than that of the surrounding hot gas. This cannot be correct because you cannot blow a bubble by sucking. In the Perseus cluster, pressure balance is reached if the extra energy required by the second method is about 200 to 500 times that of the electrons radiating at energies above 10 MHz (*6*) (The pressure of the relativistic electrons is then much greater than that of the magnetic field.) The jets are found to have a high power, with a radiative efficiency (including the lobes) of less than 0.1%.

The only unknown factor is the filling factor of the bubbles with relativistic plasma, which was assumed to be unity in the discussion above. The x-ray holes may not be empty, however, but rather filled with hotter gas. If gas in a bubble has twice the temperature of the surrounding gas with which it is in pressure equilibrium, then its density is half and its emissivity one-quarter of that of the surroundings. A hole will consequently be seen. The presence of hotter gas in the holes should in principle be detectable by deeper x-ray imaging.

The bubbles must deposit energy and magnetic fields into the cluster. This is one plausible origin for the magnetic fields found throughout the cores of clusters from Faraday rotation studies of background radio sources (*7*). The fields have an energy density of a few percent of the thermal energy density of the hot intracluster medium.

Of great interest over the past year or so has been the fate of the energy in the bubbles. The radiative cooling time of gas surrounding all the bubbles mentioned above is less than a few billion years. It might therefore be expected that the gas is getting cooler and taking part in a cooling flow. If sufficient heat can be supplied, however, then the gas might not yet cool. High spectral resolution observations with the reflection grating spectrometer (RGS) onboard the XMM-Newton satellite confirm earlier observations of a drop in temperature by a factor of 3 in this central gas compared with the outer gas, but show that there can be little gas cooler than one-third of the temperature of the outer cluster (*8, 9*).

This result suggests that gas cools from, for example, $6 \times 10^7$ K, where the cooling time is $5 \times 10^9$ years, to $2 \times 10^7$ K, where the cooling time is $10^8$ years, but no lower. This is puzzling because there is no evidence for gas accumulating at the lower temperature. Hydrodynamical simulations of jets and bubbles in hot gaseous atmospheres suggest that substantial amounts of energy can be injected into the surrounding gas (*10–13*). Such simulations have provided an explanation for a plume to the east of M87 that resembles the mushroom cloud of an atom bomb explosion. The stalk is composed of cooler uplifted gas from the center, in reasonable agreement with x-ray observation.



**Chandra image of the core of the Perseus cluster.** The high-frequency radio lobes coincide with the two central holes in the x-ray emission (the inner jets themselves point roughly north-south). The bright x-ray rims around the holes are the coolest regions in the image, and the expansion of the bubbles must therefore be subsonic (*2*). Large outer holes seen to the northwest and south are probably "ghost" lobes of buoyant plasma from earlier activity, because they are connected to the center by spurs of low-frequency radio emission. Studies of such holes allow the mean jet power of the central active galactic nucleus and its history over the past 50 million years to be determined. The nature of other outer holes is unclear; some could be even older ghosts. The energy and magnetic fields in the buoyant plasma may be of considerable importance for the intracluster medium in cluster cores.

Other bubbles have, however, been more difficult to explain. The simulations generally do not show the formation of round bubbles. The reason might be the omission of large-scale magnetic fields, which might increase the surface tension to the bubbles, thereby assisting the injection of energy by continuous weak shocks and enhancing the lifetime of the bubbles when buoyant. The outer bubble in the Perseus cluster, which is linked by a low-frequency radio spur to the inner lobes, seems to have sharp edges and does not seem to be undergoing breakup due to hydrodynamical instabilities, again implying the presence of magnetic fields.

If the bubbles retain much of the jet energy and transport it beyond the cooling region, then they are not the answer to the problem raised by the RGS spectra. Only if little energy is released into the surroundings as the bubbles grow and break up upon rising from the center can they be the explanation. An important clue is provided by several bubbles, especially those at the center of the Perseus cluster (see the figure) and in Hydra A, where the coolest gas in the whole cluster surrounds the bubbles. If the bubbles are a significant heat source, why are they the coolest regions?

Many suggestions to the cooling flow puzzle have been proposed. The central black hole, on a scale of $10^{15}$ cm, may be important for blowing bubbles and controlling the heat flow on scales of $10^{23}$ cm, but I doubt that heating by such extended feedback can be balanced to better than a factor of a few. I suspect that thermal conduction is the dominant effect on the larger scales (*14–16*). Cooling and mixing can then take over within $\sim 5 \times 10^{22}$ cm.

As expected when dealing with galaxy-sized energy and mass flows, the situation is complex. More data are clearly needed, both x-ray and (low-frequency) radio imaging and spectra. We have the opportunity to understand both the jet outflow from an active nucleus and the mass inflow from the surrounding gas. Understanding these phenomena may give us important observational and theoretical insights into some of the feedback processes present during galaxy formation.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