mare basalt, thereby excavating the underlying iron-poor highlands substrate, show that most mare plains are quite thin, usually just a few tens of meters.

The global data from Clementine and Lunar Prospector allow us to assess the regional and global distribution of the different types of mare basalt. By measuring the density of impact craters in the maria and comparing it with the ages of sites sampled by Apollo, we can map the stratigraphy of the maria globally and determine their composition, thickness, and age. This will provide a more thorough knowledge about the history and intensity of volcanism on the Moon than we have for any other terrestrial planet, including Earth, for which most volcanic resurfacing (in ocean basins) is only partly understood.

The two missions also led to the startling discovery that water ice occurs in the permanently shadowed regions near the poles of the Moon (*6*, *7*). The Moon is extremely dry—lunar samples contain no water or even hydrous minerals. Water and ice are not stable on the Moon because of the high temperatures and the lack of an atmosphere. However, ice can be trapped at the poles in zones of permanent shadow. The polar water must have been added to the Moon from an external source, probably from impacting water-bearing meteorites and cometary nuclei. The deposits thus record the history of impacting volatile elements and compounds in the inner solar system for at least the past 2 to 3 billion years.

Our knowledge of the polar deposits is, however, sketchy. Details of the amounts, composition, and physical nature of the deposits may result from future missions, which may use orbital radar imaging to measure ice extent, thickness, and purity and surface in situ measurements to determine the chemical, isotopic, and mineralogical composition of the deposits.

The global compositional data provided by Clementine and Lunar Prospector are set to revolutionize our thinking about the evolution of the Moon. Together with existing information from the Apollo and Luna samples and the 21 lunar meteorites, they are helping us to unravel the long and complex history of the Moon. The Moon is a touchstone for our understanding of the evolution of the terrestrial planets in general. Once the data are fully assimilated, many ideas and concepts in planetary science may require substantial revision.

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PERSPECTIVES: ASTRONOMY

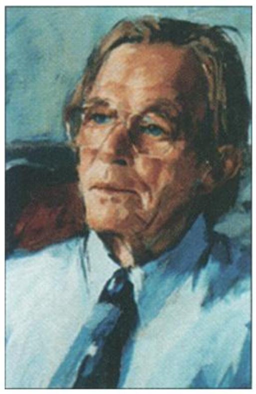
Galaxy Clusters Reveal Their Secrets

Robert Braun

Hydrogen is the most abundant element in the universe, accounting for some 70% of the total mass in baryons (particles such as protons and neutrons that experience the strong nuclear force). In addition to being ubiquitous, the hydrogen atom acts as an electric and magnetic dipole, giving rise to radiation interactions that have enormous diagnostic value in observational astronomy.

The electric dipole of hydrogen has long been exploited in astronomy. Since the recombination spectrum of hydrogen was first calculated about 100 years ago (*1*, *2*), this radiation has been used to study emissions from energized regions and absorption by quiescent regions at ever greater distances. The emission line strength is directly proportional to the number of ionizing photons. Strongly irradiated regions, such as the central regions of quasars, can thus be detected even at extremely large distances. The current record holder is at a redshift of 6.28 (*3*). Light reaching us from this distance has traveled for about 95% of the age of the universe.

The magnetic dipole properties of hydrogen give rise to a much more subtle interaction. The tiny energy difference between parallel and antiparallel spins of the proton-electron system of atomic hydrogen corresponds to a radio photon with a wavelength at rest of 21.12 cm. Van de Hulst (see the first figure) predicted in 1945 that this transition might lead to an observable phenomenon (*4*). Soon after this prediction, the emission from atomic hydrogen clouds was detected in our own galaxy, the Milky Way (*5*). On page 1800 of this issue, 50 years after this first detection, Zwaan *et al.* (*6*) report the detection of the 21-cm emission of a galaxy comparable to our own at a redshift of 0.2. At twice the distance of the previous record, this corresponds to a light travel time of about 20% of the age of the universe.



Henk van de Hulst (1918–2000)

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The 21-cm magnetic dipole radiation of atomic hydrogen is so useful because under typical conditions, its line strength is directly proportional to the total number of hydrogen atoms in the source. The radiation is not obscured by interstellar dust particles, which strongly absorb light in the visible band but not at radio wavelengths. Furthermore, high spectral resolution can be achieved relatively easily at radio frequencies. The kinematics of galaxies other than our own can thus be determined routinely with great precision and out to large distances from the centers of these galaxies. These data have helped document reservoirs of gaseous atomic hydrogen, from which new generations of stars may form, under a wide variety of circumstances. Furthermore, they have shown that the rotation velocity of galaxies does not decline with distance from the center, indicating that galaxies must contain substantial amounts of dark matter (*7*).

The great drawback of the 21-cm emission line of atomic hydrogen is its intrinsic faintness. Today's optical and near-infrared telescopes, with diameters of 3 to 10 m, can be used to observe the hydrogen recombination lines from quasars at redshifts of 6 or more (*3*). In contrast, Zwaan *et al.*'s detection of the 21-cm emission from a normal galaxy at the comparatively modest redshift of 0.2 required more than 100 hours of observation with one of the largest current radio telescopes, with an equivalent diameter of almost 100 m (*6*).

The newly detected galaxy belongs to a massive galaxy cluster named Abell

The author is at the Netherlands Foundation for Research in Astronomy, 7990 AA Dwingeloo, Netherlands. E-mail: braun@nfra.nl

2218 (see the second figure). This cluster has received considerable attention because its large concentration of mass acts as a gravitational lens that strongly bends the light from more distant galaxies behind it (*8*). Abell 2218 is one of the densest concentrations of galaxies in the local universe, containing many hundreds of galaxies within the central 3×10^6 light years. For comparison, the Local Group of galaxies to which the Milky Way belongs contains only three major galaxies within the same radius.

Abell 2218 may therefore seem like a natural target for simultaneously detecting many galaxies through their 21-cm emission within the large field of view of the radio telescope used by Zwaan *et al.* Their observation of the cluster field was sufficiently long to allow atomic gas masses as small as those of our own Milky Way to be detected. But instead of detecting the hundreds of galaxies in the cluster core, only a single galaxy was seen, some 6×10^6 light years from the core.

The surprising absence of other 21-cm detections in the Abell 2218 cluster and its surroundings provides important insights into the physical processes that shape galaxies in such a dense cluster environment. Unlike most galaxies, which are relatively isolated and evolve relatively slowly with time, galaxies in the vicinity of a dense cluster evolve very fast. Galaxy interactions and mergers are much more likely when the density of galaxies is increased. Such interactions can disrupt the stability of galaxy disks, resulting in rapid processing of the atomic gas reservoir into new stars and in the loss of stars and gas from the parent galaxies.

Cluster surprises. This image from the Hubble Space Telescope shows the dense cluster of galaxies in Abel 2218. Zwaan *et al.* provide important insights into how galaxies behave in such a cluster.

The detritus of past galaxy interactions forms a dense medium, which settles into the gravitational potential well at the center of the cluster. Any galaxy passing through this dense intergalactic medium is doomed to a rapid demise, at least as far as its gas is concerned. The large relative velocity of such a galaxy compared with the intergalactic medium results in strong compression of the galactic gas that is tightly gravitationally bound to the galaxy and complete stripping from the galaxy of the gas that is not strongly bound to it. The galaxy detected by Zwaan *et al.* is the only one in the field of view that has not yet been stripped of gas by the cluster.

Earlier indications for the efficiency of these processes were seen in 21-cm observations of the galaxy cluster Abell 2670 at the smaller redshift of 0.08 (*9*). We will likely need to study clusters at redshifts of at least 1 or 2 to witness the assembly of galaxy clusters and the early evolution of galaxies. This is one of the primary motivations for considering construction of the "Square Kilometer Array" (SKA), an internationally funded radio telescope with two orders of magnitude greater sensitivity than is now available (*10*). With some good fortune, we can hope to make this next step in much less than the 50 years it has taken us to advance from the Milky Way to Abell 2218.

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PERSPECTIVES: STRUCTURAL BIOLOGY

The xyz of ABC Transporters

Christopher F. Higgins and Kenneth J. Linton

A cell must selectively translocate molecules across its plasma membrane to maintain the chemical composition of its cytoplasm distinct from that of the surrounding milieu. The most intriguing, and, arguably, the most important membrane proteins for this purpose are the ABC (ATP-binding cassette) transporters. These proteins, found in all species, use the energy of ATP hydrolysis to translocate specific substrates across cellular membranes. The chemical nature of the substrates handled by ABC transporters is extremely diverse—from inorganic ions to sugars and large polypeptides—yet ABC transporters are highly conserved. Mutations in the genes encoding many of the 48 or so ABC transporters of human cells are associated with diseases such as cystic fibrosis, adrenoleukodystrophy, Tangier disease, and obstetric cholestasis. Overexpression of certain ABC transporters is the most frequent cause of resistance to cytotoxic agents including antibiotics, antifungals, herbicides, and anticancer drugs.

Despite years of work on both bacterial and mammalian ABC transporters, particularly the multidrug resistance transporter P-glycoprotein, it is still not clear exactly how these proteins work. Enter Chang and Roth (*1*) on page 1793 of this issue with the first high-resolution structure of a complete ABC transporter, the MsbA lipid A transporter of the bacterium *Escherichia coli*. Theirs is a remarkable achievement, given the difficulties inherent in working with these membrane proteins. To obtain this structure they overexpressed and purified more than 20 bacterial ABC transporters, and tested a phenomenal 96,000 crystallization conditions with 20 different detergents.

ABC transporters comprise four "core" domains (*2*). Two transmembrane domains (TMDs) form a pathway across the membrane through which solutes move. These domains consist of multiple membrane-spanning segments (putative α-helices) and contain the substrate binding sites. The other two domains are highly conserved nucleotide-binding domains (NBDs), which are located at the cytoplasmic face of the membrane and couple ATP hydrolysis to substrate translocation. ABC transporters are conventional enzymes that undergo a conformation change in response to ATP binding and hydrolysis. This change alters both the affinity and orientation of the substrate binding sites. X-ray structures of isolated NBDs (*3*), and a low-resolution structure of intact P-glycoprotein (*4*) have provided many insights but have failed to reveal exactly how ABC transporters translocate substrates across cellular membranes.

The authors are at the MRC Clinical Sciences Centre, Imperial College School of Medicine, Hammersmith Hospital Campus, DuCane Road, London W12 0NN, UK. E-mail: christopher.higgins@csc.mrc.ac.uk

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