ognition motif also seen in two established substrates, cardiac phosphofructokinase and endothelial nitric oxide synthase. However, the last-named substrates (unlike H2B) have hydrophobic residues between the two basic residues. Moreover, in H2B, the residue four positions after the serine is tyrosine, which was found to be unfavorable in a peptide library approach (11). Despite this imperfect fit to the recognition motif, AMPK may phosphorylate Ser[36] on H2B because it is recruited to these promoters through other interactions.

Both AMPK and phosphorylated H2B (at Ser[36]) associated not only with the promoters, but also with transcribed regions of target genes, which suggests a possible effect on elongation of transcription. When Ser[36] was changed to alanine (which prevented phosphorylation) and the mutated protein expressed, less RNA polymerase II associated with transcribed regions of a p53 target gene compared with cells expressing wild-type H2B. Moreover, expression of several other p53 targets in response to a metabolic stress decreased, and fewer cells survived the insult.

How general is this mechanism across eukaryotes? Activation of the budding yeast AMPK ortholog (SNF1) enhances transcription at a promoter at which RNA polymerase II is already recruited (12), although it is not clear whether this requires H2B phosphorylation. In budding and fission yeast H2B, the critical basic residues are conserved, but Ser[36] itself is replaced by threonine. Although threonine residues can be phosphorylated by yeast SNF1, serine is preferred (9). Thus, it remains unclear whether H2B would be a target for the yeast kinase.

The findings of Bungard et al. suggest that AMPK can modulate stages in transcription beyond RNA polymerase II recruitment by phosphorylating core components of chromatin. One possibility is that Ser[36] phosphorylation introduces two negative charges that destabilize wrapping of DNA around nucleosomes, and so directly facilitates the elongation phase of transcription. Structures of the nucleosome reveal that Ser[36] is not in a location particularly accessible to the kinase, so it is likely that phosphorylation would have

to occur on histones when they are not present in a nucleosome, or DNA may have to dissociate to allow the modification.

AMPK has generated much interest recently because of its importance in metabolism and its potential as a drug target in diabetes and cancer. The finding that it modifies chromatin adds another interesting facet to the varied effects it has on cellular function.

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ASTRONOMY

Fullerenes and Cosmic Carbon

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Hydrogen-poor conditions in a planetary nebula enable the detection of carbon-cage molecules C_{60} and C_{70}, confirming the existence of fullerenes in space.

Carbon is formed by fusion reactions in the cores of stars, and in the late stages of stellar evolution, massive stellar winds expel it into interstellar space. Atomic carbon participates in gas and solid-state chemical reactions to form a variety of organic compounds within circumstellar regions and interstellar clouds (1). Spectroscopic studies of these regions have long provided tantalizing clues to the presence of large carbon molecules that contain many aromatic rings. Candidate molecules include polycyclic aromatic hydrocarbons (PAHs), in which the rings join in flat sheets, and fullerenes, in which they form closed cages. New spectroscopic observational and analytical tools are helping to pin down which molecules are present, as well as characterize the environments that lead to their formation. On page 1180 of this issue, Cami et al. (2) report the detection, by means of the Infrared Spectrograph (IRS) onboard the Spitzer

Space Telescope, of vibrational bands of the fullerenes C_{60} and C_{70} as neutral molecules, likely attached to dust grains, in the young planetary nebula Tc 1. There was no evidence of other major carbon compounds, such as PAHs, in this hydrogen-poor environment. These observations raise important questions about the formation and evolution of fullerene compounds in circumstellar regions.

Fullerenes became candidates for interstellar carbon molecules only after their laboratory discovery by Kroto et al. (3). A few years later, Krätschmer et al. (4) reported the synthesis of macroscopic quantities of C_{60} from condensed soot. Since then, the presence of soot material in carbon-rich stars, along with the spontaneous formation and remarkable stability of the fullerene cage, strongly suggested the existence of fullerene compounds in interstellar space. Fullerenes are now made in the lab either by vaporization of graphite in a hydrogen-poor atmosphere or by photochemical processing of hydrogenated amorphous carbon.

Monitoring of soot formation shows that polyyne chains (carbon chains with alternating single and triple bonds) act as inter-
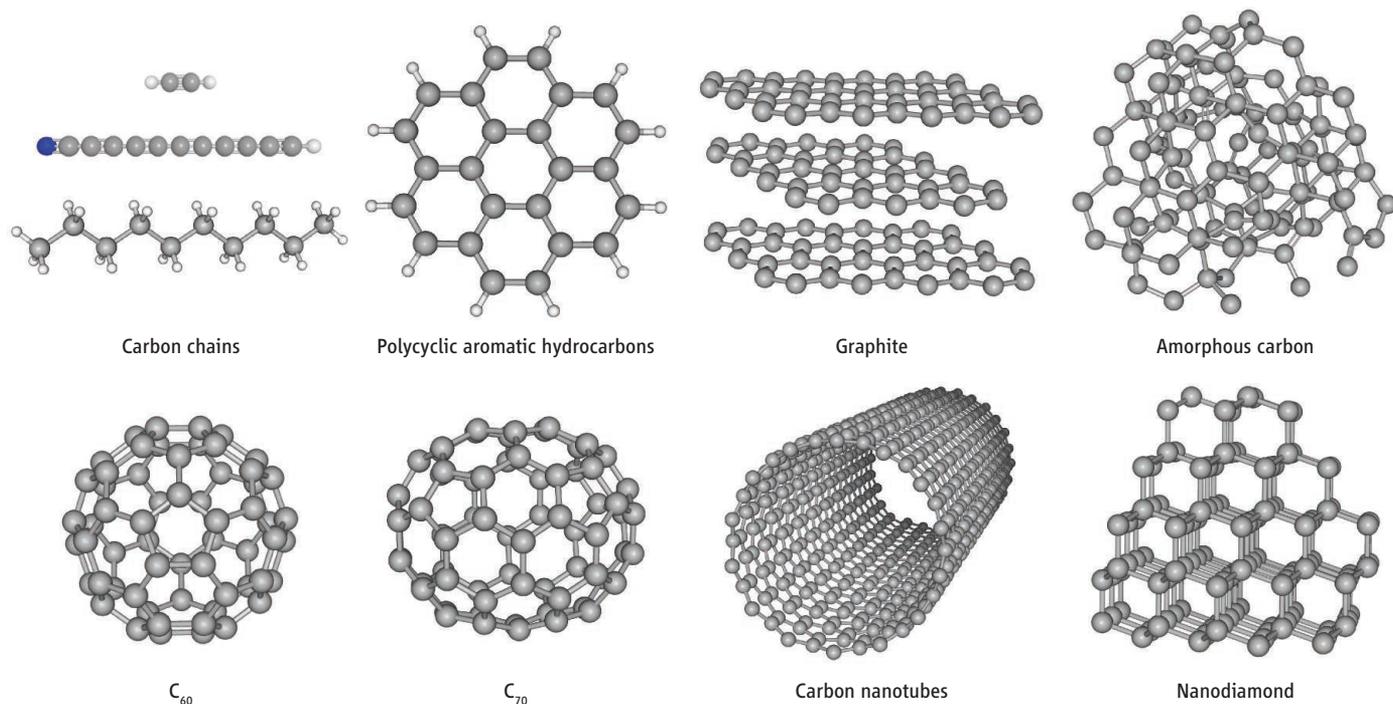
mediates and can form different products. PAHs form in the presence of sufficient hydrogen, but when hydrogen is absent, polyynes cross-link to form fullerenes (5). Recent laboratory studies forming carbon particles by gas-phase condensation reactions, such as laser pyrolysis and laser ablation, show that the temperature in the condensation zone plays a key role. Below 1700 K, the condensation by-products are mainly PAHs with three to five aromatic rings (6). At condensation temperatures above 3500 K, fullerene-like carbon grains and fullerene compounds are formed. Molecular synthesis may occur in the circumstellar environment on time scales as short as several hundred years (7).

The two strongest electronic bands, fingerprints of the C_{60}^+ ion, were discovered in the near-infrared spectra of more than 15 distant stars whose light is absorbed through diffuse interstellar clouds (8–10). The abundance of C_{60}^+ has been inferred from optical measurements to be 0.3 to 0.9% of the cosmic carbon (8, 10). Until the study by Cami et al., the search in mid-infrared wavelengths for vibrational transitions in emission of C_{60}

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Carbon chains   Polycyclic aromatic hydrocarbons   Graphite   Amorphous carbon

C_{60} C_{70} Carbon nanotubes   Nanodiamond

Carbon in space. The evidence for interstellar C_{60}^+ and detection of neutral C_{60} and C_{70} fullerene compounds in Tc 1 boosts the number of carbon allotropes present in space. Nanodiamonds and graphite are found in meteorites. Amorphous carbon may represent the main component of the solid-state carbon fraction in low-density interstellar regions. Future observations and laboratory data may lead to the identification of other fullerene compounds, such as carbon nanotubes or carbon onions. Polyynes (carbon chains) and polycyclic aromatic hydrocarbons (PAHs) are observed ubiquitously in space and are likely involved in the process of fullerene formation.

and C_{60}^+ yielded spectra that could provide only uncertain upper limits. The spectrum of Tc 1 displays clean symmetric bands that confirm the presence of fullerenes in space. The profiles of the bands, their position, and their width indicate that C_{60} and C_{70} molecules are in a neutral state. Gas-phase fullerenes ionize readily, so these molecules are likely trapped on dust grains.

The progenitors of planetary nebulae are red giant stars that have expelled gas and dust and formed a circumstellar envelope. Thermal pulses cause the ejection of their outer envelopes and create shells that cool and become regions for active gas-phase and solid-state chemistry leading to molecule formation. The core of Tc 1 provides optimal conditions for detecting the prevalence of C_{60} and C_{70} fullerene compounds in terms of temperature, recent ejection of hydrogen-poor precursor material, and a compact shell where ultraviolet excitation is low. This short phase that favors fullerene evolution may

occur in the evolution of other planetary nebulae. In the outer shell of Tc 1, hydrogen emission lines are observed at optical wavelengths, and a search for PAHs in this region could prove fruitful.

Although C_{60} and C_{70} represent only ~1% of the cosmic carbon, the analysis by Cami *et al*. and future observations will lead to a better understanding of physical and chemical processes in space, including the formation of carbon allotropes (*1*) (see the figure). Fullerene-like structures are present in "terrestrial" lab soot, and apart from circumstellar regions such as Tc 1, they are likely a component of the interstellar refractory dust fraction that dominates the inventory of cosmic carbon in diffuse clouds (*11*, *12*). Fullerene onions (formed of concentric shells of carbon) or nanotubes may also contribute to this reservoir. Direct and long-term exposure of fullerenes to cosmic rays when attached onto grain surfaces may lead to complete carbon amorphization in a few billion years. The stability of C_{60} and C_{70} fullerenes in the solid state in the interstellar medium and in solar system objects has recently been simulated with γ irradiation and He$^+$ ion bombardment (*13*).

In the interstellar gas, fullerenes may have a rich chemistry. C_{60} and C_{70} are highly electronegative and readily form compounds with electron-donating atoms (*14*). Ultraviolet irradiation in low-density interstellar clouds will ionize C_{60}, but the corresponding C_{60} dication is very stable. Hydrogenated fullerenes, as well as fullerenes forming

complexes with atoms or molecules in and outside their cages, may be present in circumstellar and interstellar environments.

The detection and analysis of Tc 1 provides a stimulus for further optical and infrared spectroscopic observations of circumstellar and interstellar fullerenes. Continued astronomical observations following these high-quality Spitzer data and related laboratory data will open a way for exploring the fascinating chemistry of these fullerenes in space environments.

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