ings support the conclusion that expanded CUG repeats in the noncoding region of RNA have a toxic gain-of-function effect on cell metabolism, regardless of whether the repeats are in the *DMPK* transcript or in some other transcript expressed in skeletal muscle.

There are several intriguing possibilities that could explain how RNA transcripts with expanded CUG repeats alter cell metabolism. The accumulation of these transcripts in numerous intranuclear foci has led to the search for proteins that interact with the repeats. One such protein, the CUG binding protein (CUGBP1), has been implicated in regulating the processing of messenger RNA (*7*). Recent in vitro studies have shown that the expanded repeat forms a single extended hairpin that binds and activates a kinase activated by double-stranded RNA (called PKR) (*8*). Additional studies are needed to determine whether CUGBP1, PKR, or other proteins that bind to triplet repeats are involved in DM.

Thus, three different mechanisms might account for the three cardinal features of DM. Cardiac conduction defects could be explained by a decrease in DMPK protein due to aberrant processing of the *DMPK* transcript. A decrease in SIX5 protein due to suppression of *SIX5* gene expression by the CTG repeat expansion in the *DMPK* gene could explain the formation of cataracts. Myotonic myopathy could be explained by the toxic gain-of-function of the expanded CUG repeats in the *DMPK* transcript. It has been further suggested that the triplet repeat expansion in the *DMPK* gene might affect expression of additional genes in this gene-rich region. For example, abnormal processing of the transcript of a nearby gene (*DMWD*) has also been shown in DM cells (*9*); as this gene is highly expressed in testis and brain, it may be implicated in the testicular atrophy and cognitive disturbances that are also associated with DM. The CpG island within the *DMPK* and *SIX5* genes is hypermethylated only in the severe congenital form of DM (*10*), further indicating that additional mechanisms might contribute to specific aspects of the disease. An attractive possibility is that the complex and variable phenotype of DM is caused by the additive effects of the toxicity of the CUG repeat in the *DMPK* transcript, decreased *DMPK* and *SIX5* gene expression, and perhaps altered expression of other genes in the vicinity of *DMPK*.

There is, however, a troublesome problem with this additive model of DM. A subset of families with the clinical characteristics of DM do not carry a triplet repeat expansion in the *DMPK* gene at the DM1 locus on chromosome 19q13.3; instead, they show linkage to a second locus (DM2) on chromosome 3q (*11*). The DM2 families have a myotonic myopathy, cataracts, cardiac conduction defects, and most of the other features characteristic of DM1. If the complex features of DM1 are caused by the additive effects of a toxic gain-of-function of the *DMPK* transcript and altered expression of neighboring genes (certainly *SIX5* and *DMPK* itself, but possibly also *DMWD* and others), then how can a mutation on another chromosome so accurately reproduce the clinical phenotype? The mutation at the DM2 locus has yet to be identified, but evidence that DM2 families show anticipation argues for another repeat expansion disease. Unless there is a parallel genetic universe with a near repetition of the DM1 locus at DM2, the unifying hypothesis must be that expressing an RNA with an expanded repeat can cause the symptoms shared by the DM1 and DM2 families. Given that Mankodi *et al.* used a skeletal muscle–specific promoter to drive the actin transgene containing the expanded triplet repeat, it is possible that expression of this transgene in other tissues would induce still other features of DM. With the Mankodi work another important piece has been added to the DM puzzle, inevitably drawing our attention to the pieces yet to be placed.


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PERSPECTIVES: SOLID STATE PHYSICS

# A Question of Dimensions

**Walt de Heer**

Carbon is the element of extremes and opposites and appears to be inexhaustible in providing new insights into the properties of matter. In the last decade, we have seen a great surge in research activity inspired by the discovery of fullerenes and subsequently of carbon nanotubes. On page 1730 of this issue, Hone *et al.* (*1*) investigate the quantized vibrations of carbon nanotubes through their heat capacities. Historically, the explanation of the temperature dependence of the heat capacity in terms of quantized vibrations remains one of the most important turning points in modern physics, ultimately culminating in the formulation of quantum mechanics.

In 1907, Einstein was unifying the nascent theory of radiation quanta, introduced by Planck, with the thermodynamics of solids. This led him to conclude that the vibrations in solids must be quantized as well, as he explained in his groundbreaking paper on "Planck's theory of radiation and the theory of specific heat" (*2*). In this paper, Einstein demonstrated that if the atomic vibrations are quantized according to Planck's relation between the quantum of energy and the vibrational energy, then the heat capacity of a solid will be temperature dependent rather than constant, as given by the Dulong-Petit law of classical thermodynamics. The temperature dependence arises essentially because at low temperatures, thermal motion is insufficient to provide the atoms with the quantum of energy needed to set them in motion. Hence, at low temperatures, they are frozen. In Einstein's picture, the heat capacity increases monotonically from zero to the classical value with increasing temperature. Einstein demonstrated the validity of the theory by comparing it with the available heat capacity data of diamond (see the figure), which, because of its hardness, exhibits these quantum effects compellingly even at elevated temperatures.

Although the trend is obviously reproduced, the theory is not complete: It can be seen already from the figure that Einstein's prediction falls short at low temperatures. Debye generalized the quantization rules to include all lattice vibrations, like standing waves and other normal modes of the system (*3*). This modified the low-temperature behavior such that in simple sys-

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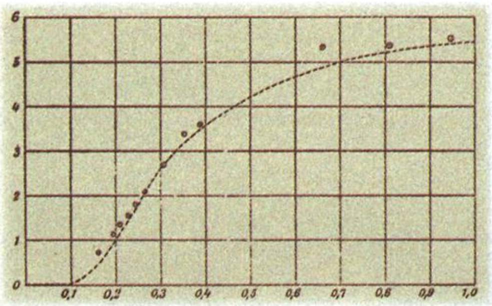
tems, the heat capacity increases as a power of the temperature. For a three-dimensional (3D) solid the power is 3, for a two-dimensional (2D) system it is 2, and for a one-dimensional (1D) system it is 1.

Graphite and diamond are almost opposite in all their physical properties. Despite its softness, the chemical bonds between the atoms in the hexagonal graphite structure are even stronger than for diamond. In contrast, the interlayer van der Waals bonds rank among the weakest in nature, and the layers easily slide over each other. If the layers were separated, then graphite would be a 2D system, with a quadratic temperature-dependent heat capacity. This is in fact observed above 150 K. From 0 to 150 K, the soft interlayer vibrations contribute to the heat capacity and eventually saturate. In this range, the temperature dependence is cubic, characteristic of a 3D solid. Hence, graphite exhibits a dimensionality crossover from 3D to 2D at 150 K.

Single-walled carbon nanotubes (SWNTs) represent yet another form of carbon (*4*). A SWNT is a single graphite sheet that is seamlessly rolled into a tube. This unique structure leads to interesting properties, which have both 2D and 1D aspects. For example, electrons are confined to the tube surface and can only move forward or backward, and SWNTs are therefore 1D conductors (it takes more energy to spin about the axis). A forward moving electron can reverse its direction only by scattering, but this requires a very specific lattice vibration (phonon) to account for the momentum and energy balance, and it occurs only rarely (*5*). Consequently, the electrons pass through the tube virtually without scattering, such that their intrinsic resistance is very low: Electrons are transported essentially without losing energy (*6*).




**Taking clues from heat capacities.** Einstein plotted the heat capacity of diamond (circles) as a function of temperature to show that atomic vibrations in solids are quantized. The temperature (*x* axis) is scaled to the Einstein temperature *qE* = 1320 K. The heat capacity (*y* axis) is given in cal/(mol K). Reproduced from (*2*).

Hone *et al.* (*1*) investigate the heat capacities of SWNTs. From a vibrational point of view, the nanotube is like a stiff rod. At low temperature, only the low-frequency 1D vibrations are excited, consisting of two transverse vibrational modes, a longitudinal mode and a twisting mode. Consequently, at low temperature, the heat capacity of the nanotube is linear with temperature. At higher temperatures, the much higher frequency modes are excited, which consist of standing waves about the axis of the tube. When these vibrations are excited, the 2D character of the nanotube comes into play, resulting in a quadratic temperature dependence. Because Hone *et al.* investigated bundles of SWNTs that are weakly connected together by van der Waals forces (as in graphite), the data show a 3D character at very low temperatures.

What is remarkable is that now, as in 1907, a heat capacity measurement provides information on the quantized nature of vibrational structure. The measurements, now as then, are represented as smooth, featureless curves of heat capacities as a function of temperature, but in fact, they reveal the underlying quantized phonon spectrum of the nanotube system as it progresses through its dimensionalities with increasing temperature. It is even more remarkable that now, as then, it is a form of carbon that provides an insight into a fundamental property of condensed matter.

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PERSPECTIVES: EVOLUTION

# When Did Photosynthesis Emerge on Earth?

David J. Des Marais

Life began very early in Earth's history, perhaps before 3800 million years ago (Ma) (*1*), and achieved remarkable levels of metabolic sophistication before the end of the Archean around 2500 Ma (*2, 3*). The great antiquity of our biosphere might indeed illustrate how easily life can arise on a habitable planet, but it also portends the challenges that confront our efforts to become intimately familiar with our earliest ancestors. The earliest sedimentary rocks have typically undergone extensive alteration by metamorphosis, taking a serious toll on microfossils (*4*). Fortunately, memories of our distant forebears are recorded not only in ancient rocks, but also in biological macromolecules (*5*) and pathways. The two records are highly complementary: The geologic record offers the absolute timing of evolutionary innovations and their environmental context, while the living biochemical record can reveal the sequence of development of key pathways and biomolecules.

On page 1724 of this issue, Xiong *et al.* (*6*) have tapped the biological record to study the evolution of photosynthesis. They have obtained new sequence information for genes involved in photosynthesis and performed phylogenetic analyses on the major groups of photosynthetic bacteria. The study better defines the molecular origins of these groups and clarifies the great antiquity of anoxygenic photosynthesis.

When our biosphere developed photosynthesis, it developed an energy resource orders of magnitude larger than that available from oxidation-reduction reactions associated with weathering and hydrothermal activity. The significance of this innovation can be illustrated quantitatively for modern Earth. Hydrothermal sources deliver (0.13 to 1.1) × $10^{12}$ mol year$^{-1}$ globally of reduced S, $Fe^{2+}$, $Mn^{2+}$, $H_2$, and $CH_4$ (*7*); this is estimated to sustain at most about (0.2 to 2.0) × $10^{12}$ mol C year$^{-1}$ of organic carbon production by microorganisms capable of using hydrothermal energy as their energy source (*8*). In contrast, global photosynthetic productivity is estimated at 9000 × $10^{12}$ mol C year$^{-1}$ (*9, 10*). Global thermal fluxes were greater in the distant geologic past (*11, 12*), but the onset of oxygenic photosynthesis most probably increased global organic productivity by at least two to three orders of magnitude. This enormous productivity resulted principally from the ability of oxygenic photosynthetic bacteria to capture hydrogen for organic biosynthesis by cleaving water. This virtually unlimited supply of hydrogen freed life from its sole dependence upon abiotic chemical sources of reducing power, such as hy-

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