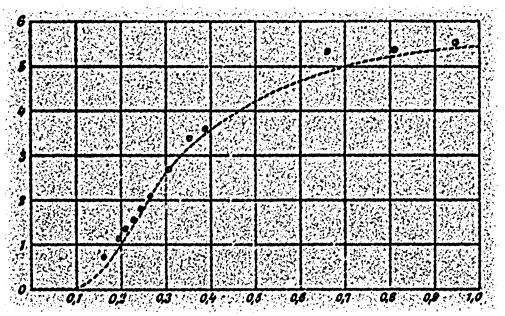
tems, the heat capacity increases as a power of the temperature. For a three-dimensional (3D) solid the power is 3, for a two-dimensional (2D) system it is 2, and for a one-dimensional (1D) system it is 1.

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.



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*).

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*).

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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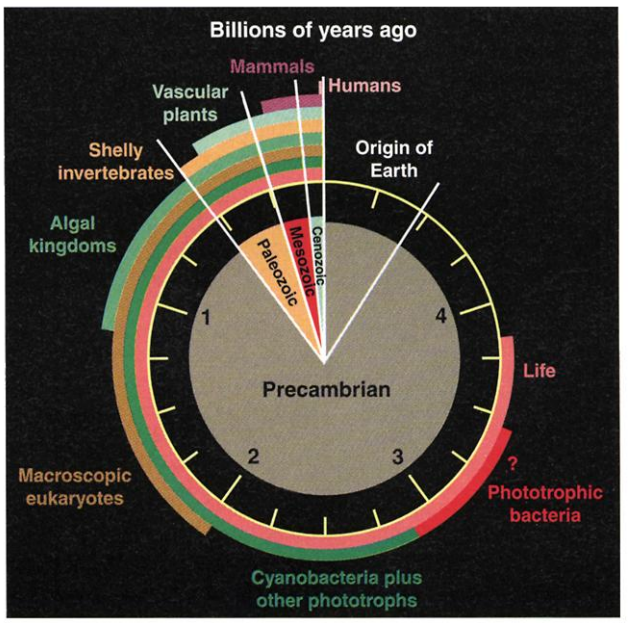
drothermal sources and weathering. Communities sustained by oxygenic photosynthesis could thrive wherever supplies of sunlight, moisture, and nutrients were sufficient.

Photosynthetic microbial communities have left a relatively robust fossil record, in part because their productivity was particularly high on stable submerged continental platforms and margins, and thus contributed to sediments with excellent potential for long-term preservation. The cyanobacterial microfossil record is robust throughout the Proterozoic (around 2500 to 543 Ma) (*3*). The record of organic biomarkers—molecules that are highly diagnostic for their parent organisms—is consistent with the microfossil record. For example, only cyanobacteria are known to synthesize 2-methyl bacteriohopanepolyols, which are transformed in sediments to 2-methylhopanes. The latter have now been identified in rocks as old as 2500 to 2700 million years (My) (*13*, *14*). The stromatolitic carbonates that were widespread along continental margins throughout the Proterozoic (*15*) have long been associated with cyanobacterial communities. Few stromatolites contain identifiable cellular fossils, but the large, Paleoproterozoic (2500 My old and younger) stromatolitic reefs that rival modern reefs in size, architecture, and extent (*16*) compel the present author to cite their development as firm evidence for oxygenic photosynthesis having become well established by 2500 Ma. Buick (*17*) also concludes that late Archean stromatolites, observed in 2700-My-old lake deposits, required oxygenic photosynthesis to develop abundantly in environmental settings that lacked evidence of hydrothermal activity.

The molecular oxygen released by photosynthesis leads to additional evidence for the antiquity of oxygenic photosynthesis. Before oxygenic photosynthesis arose, ambient oxygen levels were insignificantly low, because chemical sinks such as reduced geothermal outflows and rock weathering greatly exceeded the main abiotic source of oxygen, the photochemical dissociation of water vapor coupled with loss of hydrogen to space (*18*). The discovery of sterane biomarkers in 2700 Ma sediments (*14*) demonstrates not only the existence of eukaryotic organisms, but also that free oxygen was available for sterol biosynthesis. The extremely low $^{13}C/^{12}C$ values in 2800-My-old kerogens have been attributed to methanotrophic bacteria, which require both oxygen and methane (*19*). The substantial deposition rates of ferric iron in massive banded iron sediment formations before 2500 Ma are clearly consistent with an abundant biological source of free oxygen (*20*). Indeed, vast sedimentary deposits of organic carbon, reduced sulfide, ferric iron, and sulfate on continental platforms and along coastal margins are among the most prominent and enduring legacies of billions of years of oxygenic photosynthetic activity (*21*).

The geologic record thus offers strong evidence for the evolution of oxygenic photosynthesis before 2800 Ma. There are, however, hints of even earlier origins. The microfossil record of cyanobacteria may extend to 3300 to 3500 Ma (*22*), although the evidence for these early Archean occurrences is controversial (*23*). Stromatolites occurring in 3460-My-old carbonates and silicified carbonates of the Warrawoona Group, Western Australia, were recently described by Hofman *et al.* (*24*). These stromatolites developed in a partially restricted, low-energy shallow hypersaline basin (*25*). Hofman *et al.* (*24*) conclude that microorganisms were involved in the accretion of these stromatolites. They also surmise that microbial phototaxis (light-stimulated microbial motility) may have played a role in shaping them, but conclude that the evidence for the presence of photosynthetic biota is not yet definitive.

The carbon isotopic record of early Archean carbonates and reduced carbon is consistent with, but not yet compelling for, oxygenic photosynthesis. The isotopic patterns are consistent with isotopic discrimination by some chemoautotrophic bacteria and anoxygenic photoautotrophic bacteria, in addition to oxygenic photoautotrophs (*26*). But the absence of conclusive evidence should not be interpreted as conclusive evidence of absence. Although the early Archean fossil record contains at best a handful of demonstrated microfossils, none of which are as yet physiologically definitive, this low apparent diversity should not be interpreted too literally (*3*). It is known that as metamorphic alteration of fossil-containing rocks intensifies, the apparent diversity of remaining microfossil assemblages decreases (*4*). Conclusive evidence for oxygenic photosynthesis probably also diminishes. Current evidence for early Archean oxygenic photogenesis is perhaps not yet compelling, but it is consistent with it.



Earth's biogeologic clock. The great antiquity of our biosphere contrasts sharply with the relative youth of plants and animals. The dual geological and molecular biological records of microorganisms indicate tha our early biosphere was remarkably complex. All of the major photosynthetic groups of bacteria arose prior to 2800 Ma, perhaps much earlier.

The report by Xiong *et al.* (*6*) adds an important constraint to the perspective outlined above. The authors demonstrate conclusively for the first time that the major lineages of pigments involved in anoxygenic photosynthesis arose before the development of oxygenic photosynthesis. This indicates that the six major bacterial lineages had largely developed by the mid-Archean, around 3000 to 2800 Ma, and perhaps much earlier. The study also shows that the early biosphere passed through a stage during which even its photosynthetic populations depended exclusively on abiotic sources of reducing power. Can we recognize such a stage in the geologic record? The fossil record of anoxygenic phototrophic bacteria is poorly known, although ancient populations have been identified in much younger rocks on the basis of organic biomarkers. The presence of Chlorobiaceae in Paleozoic sediments has been inferred based on the identification of a ^{13}C-enriched aromatic polyisoprenoid (*27*). Geoporphyrins from purple sulfur bacteria have been identified in ancient shales (*28*). The survival of traces of Archean oil (*29*) offers the possibility to extend the biomarker record of anoxygenic phototrophs considerably.

As the great antiquity of photosynthesis becomes more and more apparent, it also becomes easier to envision an ancient, global biosphere sustained principally by anoxygenic photosynthesis. The global geothermal heat flow was substantially higher during Earth's first billion years (*11*), and the vigorous geothermal outgassing probably dispersed reduced chemical species throughout sunlit aquatic environments. Perhaps the substantial decline in thermal activity between 4000 and 3000 Ma created opportunities for oxygenic photosynthesis to develop. Both the geologic and living bi-

ological records of our early biosphere promise further key insights into the origin and early evolution of photosynthesis.

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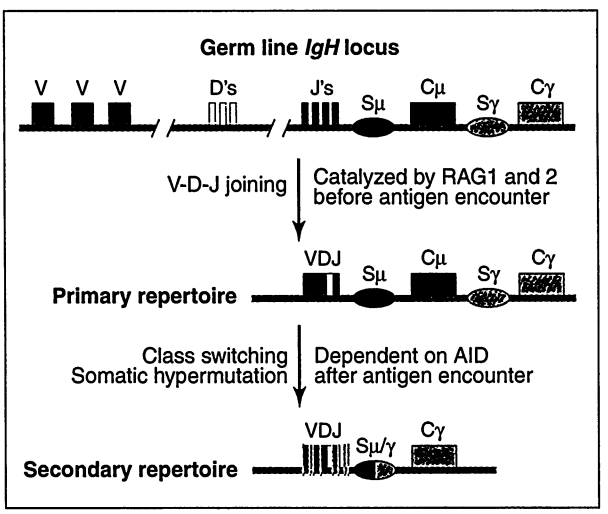
PERSPECTIVES: IMMUNOLOGY

RNA Editing AIDs Antibody Diversification?

Michael S. Neuberger and James Scott

The B lymphocytes of the immune system use multiple genetic mechanisms—gene rearrangement, somatic hypermutation, and gene conversion—to drive the generation of antibody diversity. Now, Honjo and colleagues (*1*) and Durandy and co-workers (*2*) provide evidence in a recent issue of *Cell* for an unexpected contribution to antibody gene diversification from RNA editing. The authors suggest that RNA editing is crucial for production of the secondary antibody repertoire in mature B cells.

Antigen-specific antibodies are formed in two stages (see the figure). In the first stage, a primary repertoire of immunoglobulin M (IgM) antibodies is produced in immature B lymphocytes present in the fetal liver or bone marrow. The diversity of antigen-binding sites on the antibodies expressed by these B cells is generated by gene rearrangement (see the figure). After antigen enters the body, a secondary repertoire is generated. Those B cells expressing an IgM molecule that recognizes the antigen are induced to proliferate and form germinal centers within secondary lymphoid organs. Here, two further assaults occur on the genetic integrity of antibody gene loci. The variable (V) regions (which encode the antigen-binding part of the IgM) are further diversified—this time by somatic hypermutation—allowing the generation of antibodies with improved affinity for antigen. The IgM constant region (responsible for effector activity of the antibody) is replaced by the constant region of another class of immunoglobulin (IgG, IgA, or IgE), a phenomenon termed class switching.



Generation of antibody repertoires. B lymphocytes developing in fetal liver or adult bone marrow use RAG1 and RAG2 proteins to rearrange their immunoglobulin V (variable), D (diversity), and J (joining) gene segments, producing a functionally integrated VDJ segment that is linked to the μ constant region (Cμ). This yields a primary antibody repertoire composed of IgM antibodies. Subsequent encounter with antigen causes those B cells expressing cognate IgM antibodies to proliferate, forming germinal centers in secondary lymphoid organs. Here, their rearranged immunoglobulin genes undergo class (isotype) switching and hypermutation, allowing the production of high-affinity IgG antibodies (the secondary repertoire). Class switching occurs by region-specific recombination between the switch (S) regions located upstream of Cμ and Cγ. Hypermutation introduces multiple single-nucleotide substitutions into a region of ~2 kilobases encompassing the rearranged VDJ. Deficiency in activation-induced deaminase (AID) abolishes the switching and hypermutation of the secondary repertoire.

The new work (*1*, *2*) reports that a deficiency in a single gene product, activation-induced deaminase (AID), is sufficient to obliterate generation of the secondary antibody repertoire in both human and mouse B cells. Both somatic hypermutation and class switching fail to take place, although lymphoid germinal centers are produced and are, indeed, even larger than normal.

Activation-induced deaminase was originally identified in Honjo's laboratory in a subtractive hybridization screen for genes that were activated upon the induction of class switching in a B lymphoma cell line (*3*). Examining the profiles of expressed genes revealed expression of the *AID* gene to be largely restricted to activated B cells. The sequence of the AID protein also provided a clue to its function: AID has homology to cytidine deaminases and, in particular, is closely related to Apobec-1. This protein is a catalytic component of the complex that edits apolipoprotein B messenger RNA (mRNA) and catalyzes the deamination of $C^{6666} \rightarrow U$, thereby generating a stop codon and caus-

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