

tion is induced by increasing the volume fraction (as opposed to decreasing the temperature in the case of molecular glass formers). The size of one particle is roughly the wavelength of visible light, and therefore confocal microscopy can be used to record the position of each sphere in a large sample as a function of time, thus allowing detailed questions about particle motion to be answered. The trajectories provide a motion picture of particle dynamics, in which the colloids might be regarded as stand-ins ("superatoms") for atoms or molecules. This approach shares an intellectual and technological heritage with the field of single-molecule spectroscopy (6).

Of the possible scenarios illustrated in the figure, case C is most representative of colloid motion observed near the glass transition. Consistent with inferences made from less direct measurements on molecular glass formers (7), small adjustments by a large number of particles allow structural relaxation and flow. However, case C does not even begin to do justice to the complexity of motion near the glass transition. Recent work on molecular glass formers has indicated that dynamics near the glass transition are spatially heterogeneous; that is, dynamics in some parts of the system are orders of magnitude faster than dynamics in other regions a few molecular diameters away (8, 9).

The imaging work on colloidal systems in (1) and (2) also shows heterogeneity as a dominant aspect of glass transition dynamics. Kegel and van Blaaderen (2) report a non-Gaussian van Hove function consistent with the existence of fast and slow subsets of particles on a time scale where the average particle has moved about 25% of a particle diameter. Weeks *et al.* (1) report cooperatively rearranging clusters of more than 50 fast-moving particles that seem to dominate structural relaxation [see Fig. 4A in (1)]. The properties of these clusters are similar to those found in recent computer simulations (10). Further work on colloidal systems may show which features of local structure give rise to the fast population of particles and indicate how these structures might be altered to change the properties of glass formers.

The primary issue regarding the glass transition is the cause of the slow dynamics. Contending viewpoints assert density, entropy, or underlying thermodynamic or dynamic transitions as the major factor in molecular glass formers. A secondary issue is the origin of the spatially heterogeneous dynamics observed as the glass transition is ap-

proached. It remains open whether heterogeneous dynamics are fundamentally entwined with slow dynamics or merely a side show to the main event of glass formation.

The amazing detail of the imaging experiments in (1) and (2) may succeed in answering the above questions for colloidal glass formers. Although not all features of the glass transition in colloids will be applicable to molecular and atomic liquids (11), a clear view of this particular system will certainly contribute to understanding the universal features of glass formation.

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PERSPECTIVES: EARTH SCIENCE AND EVOLUTION

Genomics and the Geosciences

Jillian F. Banfield and Charles R. Marshall

Genomics—the mapping and sequencing of genomes and analysis of gene and genome function (1)—will revolutionize the biological and possibly the geological sciences. To date, some 21 prokaryotic and 2 eukaryotic (a yeast and a nematode) genomes have been published (2), and complete sequences from hundreds, perhaps thousands, of species are anticipated in the next few years. This exploding database holds enormous promise for understanding the coevolution of life and Earth. In particular, genomic data will help to elucidate the biological contributions to modern and ancient geochemical cycles, establish the internal and external driving forces for metabolic and morphological innovation, and assess the relative importance of environmental and biological processes on the coevolution of life and Earth's surface through geologic time.

Geochemical cycles operating near Earth's surface have been altered fundamentally by microbial metabolisms ever since the origin of life. When life first evolved it did so in a context defined by its physical and chemical surroundings. Since then, geochemical cycles operating near Earth's surface have been altered fundamentally by microbial metabolisms. In modern environments, spatially and temporally resolved geochemical distribution patterns and microbial population data can be analyzed simultaneously, allowing the nature of their interdependence to be estab-

lished. Gene sequence data from large numbers of organisms may, in the long term, reveal sufficient biochemical commonality to allow the development of methods to quantify expression of metabolic pathways at the species or higher level. This will enable us to determine the extent to which chemical reactions such as sulfate reduction, iron oxidation, or organic pollutant degradation are biologically—rather than inorganically—mediated. Changes in the relative importance of biological versus inorganic processes over time and as a function of physical and chemical conditions can thus be determined. In parallel, geological information will be required to decipher the complex character of natural environments that control metabolic and microbial community structure. Some basic controls on microbial population structure have, for example, been identified in iron- and sulfur-dominated systems (3). However, in-depth analysis requires understanding of pathways for iron and sulfur oxidation, nitrogen fixation, carbon fixation, metal and acid resistance, etc. Understanding these pathways will be facilitated greatly from analysis of genomic data for members of a wide range of natural microbial populations.

Genomics also offer insights into the evolution of geochemical cycles. For example, models that argue for a predominance of oxygen-poor environments on early Earth are corroborated by molecular phylogenies that place anaerobes close to the root of the tree of life and show that oxygen-inhibited nitrogen fixation existed before the last common ancestor of all living organisms. The emission of oxygen into the atmosphere after the emergence of new, complex photosynthetic systems dramatically changed the distribution and speciation of

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numerous redox-sensitive elements (such as iron, uranium, sulfur, and manganese). This in turn led to a new partitioning of organisms between aerobic and anaerobic environments. The layered microbial communities found in biofilms and sediments reflect the progression from relatively oxidized conditions at the sediment-water or biofilm-water (or air) interface down to anoxic conditions, as electron acceptors are utilized in thermodynamically predicted sequence (4). Fossil evidence for the dramatic metabolic developments that paralleled these environmental changes is limited, but much may be learned about the order of diversification of key metabolisms from genome-based phylogenies.

Phylogenetic analyses based on whole genomes allow us to make sophisticated inferences about the metabolic capacities of the last common ancestor of living groups. However, determining when and where these ancestors lived represents a major challenge, in part because evolutionary innovations may have occurred well before they are first detected in the fossil record, if they are detected at all. However, the rock record can provide crucial information, even without well-preserved fossils. For example, recent analyses of fossil biomarkers suggest that eukaryotes (5) and cyanobacteria (6) were already abundant at least 2.7 billion years ago and 2.5 billion years ago, respectively (see the figure). In the absence of fossil data, it may be possible to use molecular clocks based on whole genomes to place absolute dates on major divergences in the tree of life.

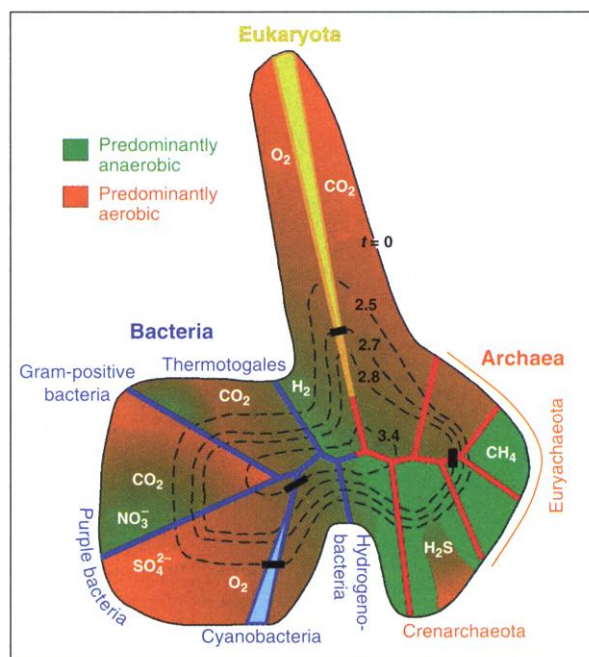
Phylogenetic analysis of genomic data will also establish the importance and frequency of gene duplication, horizontal gene transfer, and other mechanisms of genomic innovation, in the evolution of metabolic pathways of geological significance—such as nitrogen fixation, sulfate reduction, sulfide oxidation, iron oxidation, iron reduction, methanogenesis, photosynthesis, and respiration. Recent analyses of genomic sequences have highlighted the possibility of massive horizontal gene transfer in metabolic evolution (7), whereas other analyses suggest that horizontal

transfer has not been sufficiently prolific to mask the history of the major lineages in the tree of life (see the figure) (8). Analysis of genomic data in the context of the geochemical environment from which the organisms were derived may provide insights into factors controlling key events such as horizontal transfer of genetic material. For example, physiological adaptations to elevated temperature and high metal and proton concentrations restrict

organisms can respond to environmental perturbation. Understanding the modes of phenotypic evolution has now moved within our grasp (9, 10), although functional analysis is complicated by the fact that development unfolds through a series of hierarchical levels, each of which offers the opportunity for different modes of evolution. For example, the evolution of homeostatic mechanisms, some of which buffer developmental pathways from environmental perturbation, may themselves offer opportunities for new modes of evolutionary change in response to external stress (11).

The fossil record provides key insights into the evolution of life, yet ancestral forms of major groups and soft tissues are rarely preserved. However, in combination with phylogenetic data, our increased understanding of plant and animal development now makes it possible to infer the developmental capacities and establish the soft tissues likely possessed by extinct organisms, including the ancestors of the major branches of the tree of life (9). Combined with paleontological data, these advances are leading to a greatly increased understanding of key evolutionary events, such as the Cambrian explosion (12).

Genomics offer the possibility of understanding how complex organisms operate and how they evolved. The geological sciences provide the environmental and temporal context for understanding how and when key thresholds were crossed. With a rich collaboration between geosciences and biological sciences, we should expect fundamental changes in our understanding of the coevolution of the bio-, hydro-, atmo-, and lithospheres.



Correlating genomics with the geological record remains a significant challenge. The tree of life, based on the presence and absence of gene families from the 11 completed genomes of free living microorganisms (8), is placed in a temporal and environmental framework. The genomic topology is generally consistent with the 16S ribosomal RNA tree (13). Contours, labeled in billions of years (t denotes time), are schematic and are only anchored by a few minimum dates from the geologic record (indicated by black boxes). Where the geological record indicates considerable diversity within a group (5, 6), the line depicting the lineage has been expanded (yellow and blue areas). A few important metabolic by-products of the lineages are indicated.

the spatial distribution of microorganisms populating acidic solutions associated with sulfide deposits and promote cohabitation of microbial groups over geologic time scales. If genomic data reveal no horizontal gene transfer between these groups, it is probably due to the low tendency for these genes to be acquired, rather than a lack of coexistence of the relevant organisms.

For multicellular organisms, analysis of genome function is a much more daunting task than for prokaryotes. Key challenges include understanding the speed and mode of genomic evolution and how the genome functions to produce the phenotype. Answers to these challenges will lay the foundation for understanding to what extent

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