

tions in the suboxic zones, where both molecular oxygen and sulfide are nearly absent. In some cases, all of the dissolved manganese in the suboxic zone was in the +3 oxidation state, reaching concentrations of up to 4 μM .

Thermodynamic considerations indicate that manganese may play a dominant role as a catalyst in chemical cycles other than the HS^-/O_2 cycle shown in the figure. For example, the reduction of nitrate by Mn(II) and the oxidation of ammonia by MnO_2 are thermodynamically favorable in suboxic marine environments (4). Oxygen and Mn(II) concentrations do not seem to overlap in many sediment profiles, providing indirect evidence for the oxidation of Mn(II) in the absence of O_2 . However, these reactions have been difficult to demonstrate with direct measurements in environmental samples (5).

The analytical tools used in these studies are based on the assumption that the dissolved manganese is all in the reduced form. If Mn(II) is oxidized in a one-electron step to Mn(III), then the concentration of dissolved Mn [which is the sum of Mn(II) and

Mn(III) in most analytical methods] will not change. The classical paradigm would indicate that no reaction had taken place. This situation resembles our understanding of anaerobic methane oxidation a decade ago. At that time, field data suggested that a reaction consuming methane occurred, but the mechanism became clear only when new methodologies were developed (6). The work of Trouwborst *et al.* is a crucial step in moving us beyond the stalemate in our understanding of manganese cycling.

The discovery of substantial amounts of Mn(III) may also have implications for regions of the ocean that are not suboxic. The concentration of dissolved manganese decays smoothly in the deep (~3000 m) waters that flow along the oceanic conveyor from the North Atlantic into the Pacific. After several hundred radiocarbon years, manganese reaches a uniform concentration of 0.15 nM in these waters (7). In the case of Fe^{3+} , ligands such as DEF-B (“siderophores”) act as a control that drives iron concentrations in the deep ocean toward uniform val-

ues (8). There has been little plausible evidence for similar processes involving dissolved manganese, because Mn(II) interacts with organic ligands much more weakly than does Fe^{3+} . The evidence for substantial production of Mn(III) and its capability to interact strongly with siderophores introduces a new mechanism for sustaining uniform manganese concentrations in the deep ocean.

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GENOMICS

Genomics and the Tree of Life

Antonis Rokas

Only a decade has elapsed since the first prokaryote and eukaryote genomes were decoded. More than 400 genomes have been completed, some 1600 additional genomes are currently in progress, and genome-scale data sets (e.g., expressed sequence tags) are being generated at an unprecedented rate. Among the many fields feeling the impact of this genomic avalanche is phylogenetics, the discipline concerned with discovering the evolutionary interrelationships among all living organisms, an effort frequently visualized in the form of the Tree of Life (see the figure) (1). The wealth of genomic data has allowed the discovery of new molecular markers for phylogenetic reconstruction, such as rare genomic changes, but it has also presented new challenges for theoretical phylogenetic research.

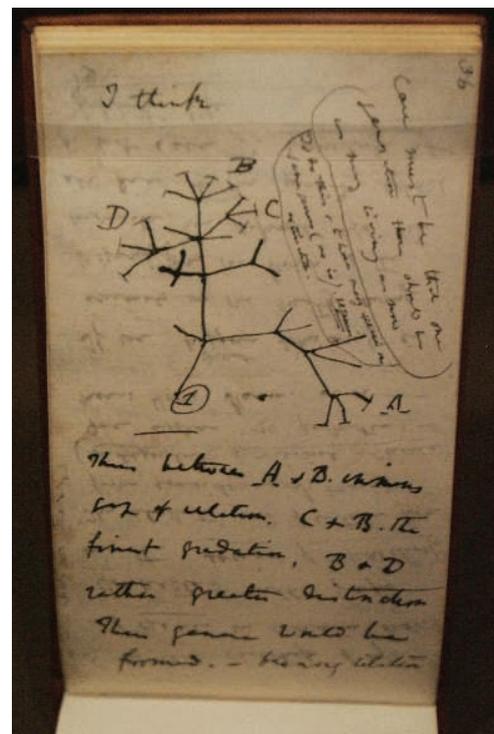
The dramatic increase in data set sizes has led, in many cases, to increased confidence in the inference of evolutionary relationships (2, 3). Data sets with small gene numbers can

generate inaccurate phylogenies because of sampling error or simply the lack of sufficient amounts of data (3). Although typical genome-scale phylogenetic studies have been rich in sequence data and thin in species number (3), as the number of sequenced genomes increases, genome-scale phylogenetic analyses are beginning to feature much larger numbers of species (4).

But further increases in data set sizes present challenges as well. Analyzing many thousands of nucleotides for hundreds or thousands of species requires substantial computational power to efficiently search among all possible trees (5). More sophisticated statistical algorithms are also needed for discovering the trees best supported by the data (6). Several clades of the Tree of Life, including the one of Metazoa, are proving difficult to resolve too (7). Most parameters of sequence evolution vary across lineages. Slight biases—amplified by the sheer volume of data—can potentially mislead phylogenetic algorithms and provide high support for the wrong trees.

Whereas the linear information in genome sequences may not always suffice, other rare features in the genomes' contents, such as sequence rearrangements or integrations of

The wealth of genome sequences—from more than 400 organisms to date—has enriched the evolutionary tree, but has also presented new challenges.



A lovely tree. Charles Darwin's famous notebook B containing the first known sketch of an evolutionary tree.

mobile genetic elements, offer some powerful alternative markers for addressing such challenging phylogenetic riddles. The use of such rare genomic changes is feasible only in a genomic context and can frequently yield remarkably precise evolutionary trees. In the mammalian lineage, this approach has led to the discovery of several new clades such as the Pegasoferae, which unexpectedly combines bats with horses, cats, dogs, and pangolins (8). Even though the use of rare genomic changes is still in its infancy, the first steps toward placing rare genomic changes-based phylogenetic reconstruction in a robust statistical framework have already been taken, thus allowing a better evaluation of their usefulness in phylogenetic reconstruction (9).

Genomics has also brought into sharp focus some thorny topics, such as the evolutionary impact of lineage sorting of ancestral genetic polymorphisms (10) and lateral gene transfer (11) on phylogenetic reconstruction. Although lineage sorting can be addressed by careful phylogenetic study design, the extensive occurrence of lateral gene transfer in prokaryotes has raised concerns as to the validity of any gene-based phylogenies for these organisms (11). Instead, gene histories in genomes that have undergone lateral gene transfer are more likely to resemble evolutionary networks and not trees. In fact, consideration of the effect of lateral gene transfer has led to searches for core sets of genes that share

the same evolutionary history and are thus likely recalcitrant to transfer between organisms (12). Such knowledge of a core set of orthologs is crucial for phylogenetic purposes, as it allows a precise estimate of the maximum amount of data available for use in evolutionary analyses. For example, it has been estimated that only 80 out of thousands of genes can be identified as orthologs across all Bacteria, Archaea, and Eucarya (the three domains of the Tree of Life) (12), a value not far from the gene number some current studies are using (4). However, given the prevalence of lateral gene transfer—mostly in prokaryotes, to a much lesser extent in eukaryotes—as well as the high frequency of gene gain and loss, questions as to whether these core gene sets are meaningful or how we can reliably identify orthology among genes remain wide open (11).

The integration of genomics data into the phylogenetics mold is just beginning. As the choice of genomes to be sequenced is increasingly guided by evolutionary considerations, and as emerging sequencing technologies promise to drop costs even lower, the reach and impact of genomics to non-model organisms is rapidly extending. Of course, with about 2 million known species of organisms and another 10,000 being discovered each year, the fraction of species for which genome-scale data are available is truly minuscule. Although phylogeneticists have been publishing an aver-

age of 15 phylogenetic trees per day, less than 1% of known species have been part of any sort of phylogenetic analysis (1). Given the breadth of organismal diversity, the gene-scale era of phylogenetics is still an invaluable asset to the pursuit of the Tree of Life. Comparative genomics, with its ability and potential to vastly increase both the amount and type of molecular data available for a small but critical fraction of biodiversity, is bound to play an increasingly important role in efforts to assemble a robust picture of the Tree of Life.

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PLANETARY SCIENCE

Merging Views on Mars

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In 2003, three spacecraft went to Mars. One was the European Space Agency's Mars Express orbiter, whose primary goal was to map the planet with a suite of remote sensing instruments. The other two were Spirit and Opportunity, the two rovers of NASA's Mars Exploration Rover (MER) mission. Their job was to explore two locations on the martian surface in detail, searching for evidence of past environmental conditions and their suitability for life.

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Three years after launch, and more than 2 years after arrival at Mars, all three spacecraft are still going strong. Along the way, they have acquired complementary data sets that reveal new information about the history of martian water and the possibility that the planet once harbored habitable conditions. Recently scientists from the OMEGA (Observatoire pour la Mineralogie, l'Eau, les Glaces et l'Activité) spectral imager team and the MER Athena science team met together to compare and merge results from their two investigations for the first time (1). Each group brought data from a sophisticated array of instruments and detectors (2, 3) to the workshop.

Spirit landed in Gusev crater on 4 January 2004. Gusev was chosen because a large dendritic channel, Ma'adim Vallis, debouches

Rover observations and global satellite data show that the surface of Mars was wet and acidic early in its history, but rapidly became dry and oxidizing.

into it, suggesting that a lake once occupied the crater. The rover, however, did not find sedimentary rocks at its plains landing site. Instead, all of the rocks there were olivine-rich basalts, indicating that any lacustrine sediments had subsequently been buried with lava. The basalts were largely unaltered, implying little aqueous activity at the site since their emplacement. Spirit spent all of its 90-sol (4) originally scheduled mission exploring lava plains (5).

Circumstances changed on sol 156, when Spirit reached the base of the Columbia Hills, 2.5 km from the landing site. These hills, which predate the lava plains, show remarkable geologic diversity. In more than 700 sols of exploration, Spirit has identified more than 10 chemically distinct rock types there. Most are impact ejecta or volcanic materials, many