

species contains the most abbreviated sterol pathway yet identified in any organism. Experiments show that the major sterols in Gemmata are lanosterol and its uncommon isomer, parkeol. In bacteria, the sterol biosynthesis genes occupy a contiguous coding region and may represent a single operon. Phylogenetic trees show that the sterol pathway in bacteria and eukaryotes has a common ancestry. Gemmata may retain the most ancient remnants of the pathway's origin, and it is likely that sterol biosynthesis in eukaryotes was acquired through gene transfer from bacteria. However, this work indicates that no known prokaryotes could produce the 24-ethyl steranes found in Archaean rocks(1). Therefore these compounds remain indicative of the presence of both eukaryotes and O₂ at 2.7 Ga. 1. J. J. Brooks, G. A. Logan, R. Buick, R. E. Summons, (1999) Science 285, 1033-1036.

U52B-07 1510h INVITED

Bacterial Bolsheviks: PS II and the Evolution of the Oxygenic Revolution

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After the rise of life itself, the most radical transformation of Earth's biogeochemical cycles was the transition from an anoxic to an oxic world. Though various studies have suggested O₂ made its first bulk appearance in the atmosphere some time between 3.8 and 2.1 Ga, virtually all analyses agree the production of large quantities of free O₂ was triggered by the evolution of oxygenic photosynthesis. We suggest the oldest strong geological evidence for O₂ is the 2.22 Ga Kalahari Mn member of the Hotazel BIF (1), as in the oceans only free O₂ can oxidize soluble Mn(II) into insoluble Mn(IV). Some have argued, however, that oxygenic cyanobacteria had originated by 2.7 Ga. The ~500 Myr "gap" has often been interpreted as the timescale for gradual evolutionary improvement of the O₂-generating system. Biochemical and genomic analyses of photosynthetic bacteria indicate that photosystems I and II, which operate together in cyanobacteria, had a long history of parallel development. Green sulfur bacteria and heliobacteria use PS-II, while green non-sulfur and purple bacteria use PS-I; none can use H₂O as an electron donor. Recent genetic analyses show lateral gene transfer was rampant among photosynthetic lineages (2). Moreover, extant cyanobacteria shut down PS-II in the presence of an alternative electron donor like H₂S. This suggests PS-I and PS-II came together with their functions intact. Hence, most debugging' of the two systems predates their merger in the ancestor of modern cyanobacteria. The time interval between the lateral transfer events and the evolution of oxygenic photosynthesis could thus have been geologically short. We suggest the ~500 Myr "gap" may result from misinterpretations. The presence of oxygenic photosynthesis is uncertain before the deposition of the Hotazel formation, in the aftermath of the Makganyene glaciation (1). A simple model of nutrient and reductant fluxes argues that, once triggered, the oxygenation of a reducing surface environment warmed by a CH₄ greenhouse (3) should occur fairly rapidly, within ~ 10 Myr. The trigger requires both the evolution of cyanobacteria and sufficiently high nutrient (mainly P) fluxes to allow O₂ production to overwhelm reductant fluxes. P flux into the oceans in glaciated worlds correlates with increased continental weathering during glacial intervals (4). Thus, were cyanobacteria present during the Huronian glaciations, which predate 2.22 Ga (5), these glaciations should have triggered the oxygenation event. Instead, the oxygenation event seems to correlate with the Makganyene glaciation, at 2.22 Ga (6). The appearance of red beds in the Upper Timeball Hill formation directly underlying the Makganyene diamictite supports this interpretation. As would be expected from a glaciation associated with the destruction of a CH₄ greenhouse, paleomagnetic data indicate the Makganyene glaciation was a global Snowball event (7). Cyanobacteria appear to have evolved in the short interval between the Huronian glaciations and the Makganyene glaciation. The lengthy delay between the earliest life on Earth and the appearance of cyanobacteria suggests that the oxygenic revolution was a fairly low probability event; planets with oxygenic biospheres may be quite rare. 1. J. L. Kirschvink et al., PNAS 97, 1400-1405 (2000). 2. J. Raymond et al., Science 298, 1616-1620 (2002). 3. A. A. Pavlov et al., JGR 105, 11981-11990 (2000). 4. K. B. Föllmi, Geology 23, 503-506 (1995). 5. S. R. Noble, P. C. Lightfoot, Can. J. Earth Sci. 29, 1424-1429 (1992). 6. D. H. Cornell et al., Precamb. Res. 79, 101-123 (1996). 7. D. A. Evans et al., Nature 386, 262-266 (1997).

U52C MCC: 3001-3003 Friday 1600h

Evolution of Biogeochemical Cycles II

Presiding: P Falkowski, Institute of Marine and Coastal Sciences, Rutgers University; M New, NASA Headquarters

U52C-01 1600h

The Co-evolution of the Nitrogen and Oxygen Cycles on Earth

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The rise of free oxygen in the Earth's atmosphere, approximately 2300 Ma appears to have been delayed by approximately 400 Myr from the emergence of oxygenic photoautotrophs. One possible constraint of the oxidation process was the interaction of oxygen with other, essential, nutrient elements. We hypothesize that a negative feedback between the nitrogen cycle and oxygen evolution retarded the rate of oxygen production and limited final concentration of oxygen in Earth's Archaean atmosphere. To examine the feedback processes, we developed a coupled biogeochemical model of the oxygen, nitrogen, and carbon cycles and examined how the behavior of these three elements is related to ocean circulation, the relative area of continental shelves, and the initial concentration of phosphate in the ocean. The model results suggest that the nitrogen cycle poses a constraint on the oxidation status of Earth. That constraint continues to the present time.

U52C-02 1615h

The Use of Manipulations in Studies of Nitrogen and Carbon Cycling in Modern Microbial Mats

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Modern microbial mats, laminated microbial communities analogous to the oldest known forms of benthic ecosystems on Earth, contain an invaluable biogeochemical and molecular record of processes and microorganisms thought to be important in their formation over geologic time. We are conducting manipulations of environmental conditions thought to be important in the ecology of microbial mats in order to better understand mat biogeochemical cycling. We present here the results of long-term (ca. one year) manipulations of nutrient and sulfate concentrations in water overlying mats kept in a greenhouse. As the element often limiting production in the marine environments, nitrogen takes on special significance in microbial mat ecology. Microbial mats are often the sites of high rates of N fixation (the energetically expensive conversion of atmospheric dinitrogen into a biologically useful form) and mats host an extremely diverse assemblage of nitrogen fixing microorganisms. Incubation of mats in the absence of nutrient additions resulted in the developments of higher rates of nitrogen

fixation as the community of nitrogen fixing microorganisms responded to the shortage of nitrogen. Additions of phosphorus additionally stimulated nitrogen fixation whereas additions of combined nitrogen suppressed nitrogen fixation. We have also incubated modern microbial mats at the lower sulfate concentrations thought to be present in the Archaean and early Proterozoic Eons. On the modern Earth, high concentrations of sulfate enable sulfate reducing microorganisms to out-compete methanogens for substrates, consequently dominating the degradation of organic carbon in the marine environment. However, very high rates of microbial methane production are implicated in generating the high atmospheric methane concentrations thought necessary to counteract the effects of a less luminous sun during the Archaean and early Proterozoic. Lowered sulfate concentrations in our manipulations did result in lowered rates of sulfate reduction, and an increased (up to six fold higher) flux of methane from these mats. The quantitative importance of methanogenesis in carbon remineralization, even under low sulfate conditions, was, however, relatively small. The results of these experiments demonstrate the utility of environmental manipulations in examining biogeochemical cycling in the environments in which they evolved, namely complex communities of microorganisms.

U52C-03 1630h

Mathematical simulation of the diel O₂, S, and C biogeochemistry of a hypersaline microbial mat

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The creation of a mathematical simulation model of photosynthetic microbial mats is an important step in our understanding of key biogeochemical cycles that may have altered the atmospheres of early Earth and of other terrestrial planets. A modeling investigation is presented here as a tool to utilize and integrate empirical results from research on hypersaline mats from Baja California, Mexico into a computational system that can be used to simulate biospheric inputs of trace gases to the atmosphere. An early version of our model calculates fluxes and cycling of oxygen, sulfide, and dissolved inorganic carbon (DIC) via abiotic components and via the major bacterial guilds: cyanobacteria (CYA), sulfur reducing bacteria (SRB), purple sulfur bacteria (PSB) and colorless sulfur bacteria (CSB). We used generalized monod-type equations that incorporate substrate and energy limits upon maximum rates of metabolic processes such as photosynthesis and sulfate reduction. We ran a simulation using temperature and irradiance inputs from data collected from a microbial mat in Guerrero Negro in Baja Mexico. Model oxygen, sulfide, and DIC results compared well with data collected in the field mats. A divergence from the field data was an initial large negative DIC flux early in the morning and little flux into the mat thereafter in the simulation. We hypothesize that this divergence will be reduced or eliminated if the salinity of the water surrounding the mat were used as an environmental input and as a limit to photosynthesis rates. Salinity levels, organic carbon, methane, methanogens and green non-sulfur bacteria will be added to this model before it is incorporated into a global model to simulate geological time scales.

URL: <http://geo.arc.nasa.gov/sge/casa/>

U52C-04 1645h

Not Just a Poison: Microbes That Derive Energy From Arsenic and Their Linkages to the C, N, and S Cycles.

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Elements that are abundant in the Earth's crust and the microbes that derive energy from them have been the focus of much research in geomicrobiology. However, some trace elements also have significant biogeochemical cycles that are mediated by microorganisms, but the wider implications of these phenomena have generally been overlooked. This has been the case for arsenic. Arsenic is a toxicant owing to its action as an analog of its Group VB neighbor phosphorus. However, a surprising finding was that a wide diversity of anaerobic prokaryotes gain energy for growth by using arsenate as their electron acceptor, and that they are broadly distributed in nature. They carry out the dissimilatory reduction of arsenate to arsenite while oxidizing organic matter (or hydrogen). Since the electrochemical potential of the arsenate/arsenite couple is 60 mV, it acts as an oxidant of more reduced species like sulfide (~ 220 mV). Some arsenate

respirers oxidize sulfide, and in doing so fix CO₂ into cellular material. Arsenite can be oxidized back to arsenate by aerobic chemoautotrophic microorganisms, or by anaerobes that use nitrate (440 mv). In addition, heterotrophic arsenate-respirers can carry out the reverse reaction, especially in arsenic rich environments like Mono Lake. The possible evolutionary significance of these phenomena and speculation about their occurrence elsewhere in the Solar System will be discussed.

U52C-05 1700h

Dynamics of the Neoproterozoic Carbon Cycle

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The Neoproterozoic (1000-543 Ma) record of the isotopic composition of inorganic carbon exhibits extraordinarily large fluctuations, of a magnitude not seen in the ensuing Phanerozoic (543 Ma–present). Thus a key feature of the long-term carbon cycle changed at the Proterozoic-Phanerozoic boundary. Moreover it almost certainly was related, but not necessarily causally, to the Cambrian radiation of multicellular animal life that began at that time. Here we address these changes quantitatively, by a dynamical interpretation of the carbon-isotopic record. Information on the evolution of the carbon cycle is encoded in the coupled fluctuations of the isotopic content of inorganic carbon and the fractionation between inorganic and marine organic carbon. Whereas significant fluctuations in the Phanerozoic record are consistent with steady-state models of the carbon cycle, their larger Neoproterozoic counterparts are not. The Neoproterozoic records can be well understood, however, as deriving from the nonsteady dynamics of two reactive pools of carbon. The lack of a steady state is traced to an unusually large oceanic reservoir of organic carbon. We suggest that the most significant of the Neoproterozoic negative carbon-isotopic excursions resulted from increased oxidation of this reservoir, possibly as a result of severe global cooling. The terminal Neoproterozoic isotopic event, at the Proterozoic-Cambrian boundary, signals the final diminution of the reservoir, a process that was likely initiated by evolutionary innovations that increased export of organic matter to the deep sea. The terminal event also signals a change from a carbon cycle evolving dynamically, permanently out of steady state, to one evolving quasistatically, from one steady state to another.

URL: <http://segovia.mit.edu/publications/2003/neoprot.abs.html>

U52C-06 1715h

Geosphere-Biosphere Feedbacks as a Trigger for the Cambrian explosion

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A new hypothesis for the cause of the Cambrian explosion is presented. The Cambrian explosion 542 Myr ago is characterized by a sudden increase of biomass and a rapid cooling, which amplified the spread of complex multicellular life. The evolution of the planet Earth is described by the co-evolution of the geosphere-biosphere system. A conceptual model for the global carbon cycle of the Earth containing the reservoirs mantle, ocean floor, continental crust, continental biosphere, the kerogen, as well as the aggregated reservoir ocean and atmosphere is presented. In this study the evolution of the mean global surface temperature, the biomass, and reservoir sizes over the whole history and future of the Earth under a maturing Sun is investigated. Here we specify our previously published Earth system model (Franck et al., 2002) by introducing three different types of biosphere: procaryotes, eucaryotes, and complex multicellular life. They are characterized by different temperature tolerance windows and biotic amplification factors of silicate weathering. The biotic enhancement of weathering by complex multicellular life adds an additional feedback to the system and triggers the Cambrian explosion. The Cambrian explosion was mainly driven by extrinsic environmental causes, i.e. a gradual cooling of the Earth. The Cambrian explosion was so rapid because of a positive feedback between the spread of biosphere, increased silicate weathering, and a consequent cooling of the climate. The environment itself has been actively changed by the biosphere maintaining the temperature conditions for its existence. Furthermore, it can be shown that the coupled geosphere-biosphere system exhibits bistability: there exist two stable model solutions for a certain interval of the biotic enhancement factor, one solution with and one without complex multicellular life. In particular, cooling events in the Neoproterozoic, could force a premature appearance of complex multicellular life. Frank, S., Kossacki, K.J., von Bloh, W., and Bounama, C., 2002. Long-term evolution of the global carbon cycle: historic minimum of global surface temperature at present. Tellus 54B, 325-343.

U52C-07 1730h

Biogeochemical Regime Shifts in a Model of the Subtropical Oceans

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Recent observations show that the inorganic nitrogen to phosphorus ratio in the ocean's subtropical gyres changes on interannual to decadal timescales in association with biogeochemical regime shifts. Here in a highly idealized model of the subtropical oceans we illustrate how competition between diazotrophs and other phytoplankton might lead to such changes and regime shifts on decadal timescales. The simple two layer (mixed layer and thermocline) model exhibits a sustained oscillation in which the surface subtropical ocean switches between phosphorus and nitrogen limited regimes, and the role of nitrogen fixing organisms waxes and wanes on timescales of decades. While the physical communication between surface and thermocline waters sets the timescale of the oscillation there is no interannual

or decadal variability in the models circulation. The decadal oscillation in this idealized model is due to biogeochemical interactions and not a response to climate change. We will describe the model and its behaviour in detail and discuss the implications for observed changes in the subtropical oceans of the North Atlantic and North Pacific.

U52C-08 1745h

Biogeochemical Cycles and the Search for Life Beyond the Solar System.

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NASA and ESA are currently supporting the development of missions to directly detect and characterize Earth-sized planets around other stars. These missions, slated for launch in the 2015 time frame, will provide our first opportunity to spectroscopically study the global characteristics of Earth-like planets beyond our solar system, and to search for the first clues as to whether these planets are currently habitable, or support life. Concepts for subsequent missions will build upon these initial discoveries, but provide higher spectral resolution for improved characterization of the worlds that we find. To inform this mission development, it is important that we understand the global characteristics of planets that support life, at each stage in their evolutionary development. Consequently improvements in our understanding of the evolution of Earth's biogeochemical cycles and the effect that life has on planetary characteristics on a global scale, has direct relevance to the search for life beyond the solar system. This talk will describe current work by the Virtual Planetary Laboratory of the NASA Astrobiology Institute to provide the framework for understanding the links between biogeochemical cycles and detectable global parameters over the course of the Earth's history, and for a range of plausible extrasolar terrestrial planet types. Specifically, we will describe two complementary modeling efforts: 1) ongoing efforts to characterize the cycles of S, C and O globally on early Earth using zero dimensional ecological models as well as 2) the initial development of a mosaic of regional models that will characterize the cycles of a series of biologically relevant elements in several different sorts of environments. The ecological modeling, which is essentially zero dimensional, builds on a heritage of models that have been used to estimate the range of plausible conditions in early Earth systems that lack strong empirical constraints. These models will be used to explore how highly parameterized versions of biogeochemical systems respond to perturbations. Such exploration will help to determine the conditions used in testing the full model. Ultimately, we will replace the simpler ecological models with a mosaic of modules that will describe the biogeochemical and physical behavior of elements as they cycle in environments ranging from the highest mountains to the abyssal ocean plains. These modules will synthesize the state-of-the-art in reactive transport modeling of biogeochemical systems.

URL: <http://vpl.ipac.caltech.edu>

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