SPOTLIGHT

LINKING GEOMICROBIOLOGY WITH ICHNOLOGY IN MARINE SEDIMENTS

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In the last few years, the wealth of new information on microbial diversity, metabolic capabilities, and environmental constraints has led to significant insights into the ways in which microbes interact with their local environments. Indeed, microbes are integral to mineral dissolution, sorption and precipitation reactions, aqueous redox processes, and, ultimately, global elemental cycles. In this regard, they have helped shape our planet over the last 4 billion years and made it habitable for higher forms of life.

The role of microbial communities in driving the major sedimentary diagenetic reactions is one aspect of geomicrobiology that has received significant attention. Through various chemoheterotrophic pathways, microorganisms are ultimately responsible for the conversion of organic carbon to CO_2 and CH_4 (see Konhauser, 2007). In marine sediments, the

more labile materials are degraded in the shallow subsurface on time scales of days to years; more refractory materials are broken down deeper in the sediment on time scales of hundreds to thousands of years, while the most resistant materials, precursors to fossil fuels, are transformed only on time scales of millions of years. Pore-water and mineralogical changes during diagenesis are also directly related to the bacterial reduction of aqueous species (O_2, NO_3^-, SO_4^{2-}, CO_2) or metal oxyhydroxides in the sediment. The terminal electron-accepting process that occurs at any given depth depends on which oxidants are available and, in situations in which multiple electron acceptors are present, as in the uppermost sediment layers, on the free energy yield of the specific reaction. The decomposition of freshly deposited organic material thus proceeds in a continuous sequence of redox reactions, with the most electropositive oxidants being consumed at or near the surface and progressively poorer oxidants being consumed at depth, until the labile organic fraction is

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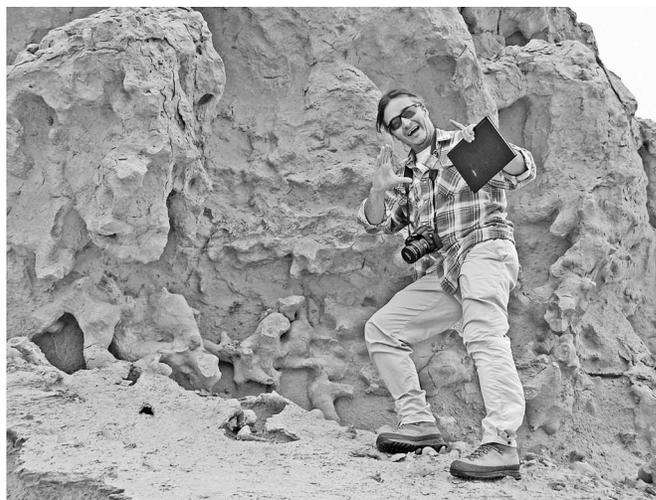
Kurt Konhauser (left) graduated with a B.Sc. in Geology at the University of Toronto and then went on to complete his Ph.D. in Earth Sciences at the University of Western Ontario under the supervision of Dr. Bill Fyfe. His first faculty position was in the Earth Sciences Department at the University of Leeds before moving to take on a Canada Research Chair in Geomicrobiology in the Department of Earth and Atmospheric Sciences at the University of Alberta. His research interests center on the interactions between microorganisms and their environment, from understanding microbial metal sorption, biomineralization, and weathering reactions to how microbes affect sedimentary geochemical cycles. His studies on modern systems form the basis for his work on the preservation of early life forms as microfossils and the formation of Precambrian banded iron formations. He is also editor-in-chief for the journal *Geobiology* and just recently wrote a book entitled *Introduction to Geomicrobiology,* published by Blackwell.

Murray Gingras (right) received his diploma in Mechanical Engineering Technology from the Northern Alberta Institute of Technology in 1987, his B.Sc. degree from the University of Alberta in 1995, and his Ph.D. from the University of Alberta in 1999. He has worked professionally in the hydrocarbon industry, at the Northern Alberta Institute of Technology and as an assistant professor at the University of New Brunswick. He is presently an associate professor in the Department of Earth and Atmospheric Sciences at the University of Alberta. His research focuses on applying sedimentology and ichnology to sedimentary rock successions, as a paleoecological tool, a reservoir-development tool, and in process sedimentology.

Cover explanation: Plio-Pleistocene Roe Calcarenite, Nullarbor Plain, Western Australia (see James and Bone, herein, p. 343). Top left: thin section photomicrograph (see Fig. 5A in James and Bone, herein); top center: mollusk-rich biota; top right: Bivalve-*Marginopora* limestone; bottom: interpretation of the marine seagrass environment at the time of deposition (see Fig. 11 in James and Bone, herein).
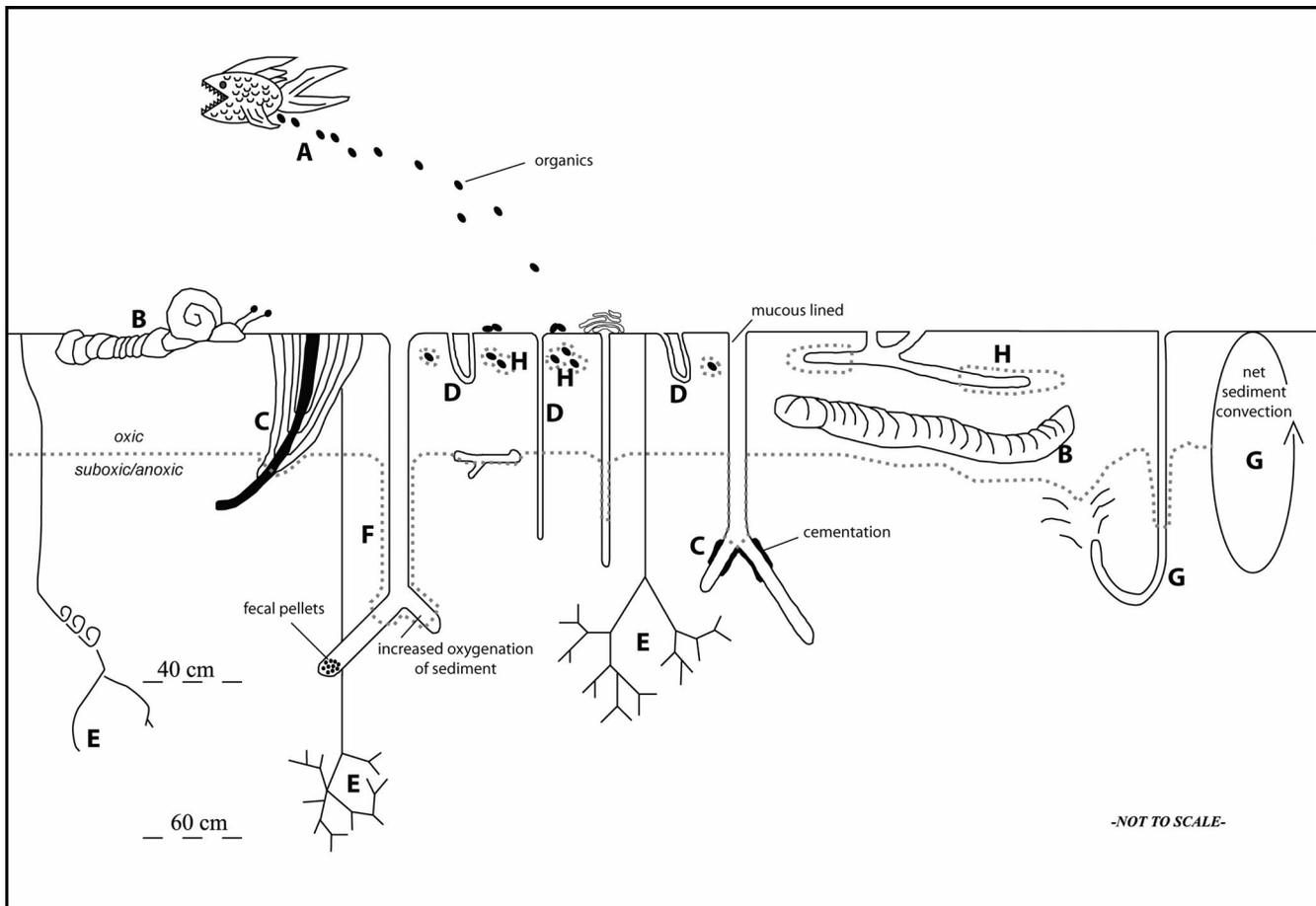
FIGURE 1—Schematic representation of the biogeochemical landscape in burrowed sediment, showing a partial range of burrow types. A) Initial organic input is derived from the water column. This source (pelagic in general) is the base of the food pyramid for the sediment-dwelling community. B) Some sediment grazers (snails and urchins shown here) enrich the sediment in mucous as a result of the animal's passage, dominantly in the oxic layers. Following decomposition, mucous may provide a secondary organic source for chemoheterotrophic microbial communities. C) Organic-rich linings (commonly composed of fecal mud) on worm and arthropod burrows are another source of organic substrates. They help stabilize the burrows and serve as reactive surfaces for metal sorption and diagenetic mineral (cement) formation. D) Small, shallow, unlined burrows probably have little impact on the long-term biogeochemical character of the sediment. E) Organic substrates may be mined at depth. F) Increased oxygenation of burrow waters, and the surrounding sediment, facilitates the subsurface oxidation of reduced solutes and mineral phases. G) Burrowing convects reduced solutes and mineral phases to the seafloor where they are reoxidized. H) Anoxic microniches can form in the oxic layers due to anaerobic respiration of labile organic substrates, particularly in fine-grained sediment.

exhausted and the deeper sediments are left with a composition very different from the sediments originally deposited. Inorganic by-products of chemoheterotrophy (e.g., HCO_3^-, Mn^{2+}, Fe^{2+}, NH_4^+, NO_2^-, HS^-, HPO_4^{2-}, CH_4) seldom accumulate to very high concentrations. Instead, there is a net transport of these reduced species from deeper sediment towards the seafloor, where resident chemolithoautotrophic bacteria use them as reactants in their metabolism, for example, oxidation of NH_4^+ to NO_3^- or HS^- to S^o or a sulfoxy anion, such as SO_4^{2-}. Alternatively, their presence in pore waters may trigger important abiotic reactions between solid and dissolved phases, leading to secondary mineral precipitation and cement formation, for example, phosphates, iron sulfides, amorphous silica, and various carbonate phases.

Although the fundamentals underpinning microbial metabolisms are well established, it is becoming apparent that the sequential scheme of biogeochemical zones is an oversimplification. One reason is that the top few centimeters of sediment are home to a number of animals. They physically disrupt the surface sedimentary layers through their bioturbating activity (Fig. 1), including burrowing and mixing of fresh sediment with older sediment; grazing and mining of intact organic remains, leading to disintegration and higher surface area for microbial respiration; and the ingestion of refractory organic carbon, which may lead to the excretion of more labile fecal pellets (Lee, 1992). Bioturbation also has

an influence on the solid phase and pore-water properties of sediment by increasing the transport of diagenetic reactants and products across the sediment-water interface, which then affects the oxidation of redox-sensitive elements. For instance, irrigation of worm burrows with oxygenated seawater results in increased downward and lateral diffusion of O_2 into surrounding sediment and the concomitant oxidation of pyrite and enhanced diffusive loss of HS^- (Berner and Westrich, 1985). Subsurface flushing with oxygenated waters similarly influences nitrification and the oxidation of Fe(II) and Mn(II). In the case of Fe cycling, as long as ferric oxyhydroxides persist, phosphate remains adsorbed to the mineral surface and is thus unavailable to pore waters (Krom and Berner, 1981). Surficial sediments, consequently, cannot be considered a homogeneous medium dominated by one-dimensional vertical diffusion. They are, instead, heterogeneous and intensively mixed with a convoluted spatial distribution of biogeochemical zones that are impossible to accurately resolve during sampling (Aller, 1980).

In tidal flats, the inner shelf, and in many bays and estuaries, the distribution of burrowing animals results from a combination of such random events as larval recruitment, longer-term interspecies relationships, and evolutionary trends, as well as environmental conditions, including the salinity, temperature, oxygenation, and hydraulic energy prevalent at the time of animal colonization (e.g., Pemberton and Gingras, 2005). The

number of burrows present in an average sediment may range from $\sim$100 per m² with larger animals such as shrimp and lugworms, to more than 50,000 per m², with smaller animals such as threadworms or amphipods (Gingras et al. 1999). Crucially, those burrows represent an ideal micro-environment for microbes because many are lined with organic materials, usually polysaccharides and proteins, that serve both as a substrate for heterotrophic species and as a reactive interface for the sorption of dissolved solutes and secondary mineral precipitation. Some estimates suggest that microbial communities in marine sediments are near 1×10^8 cells per gram of sediment (Rajendran et al., 1992) but can exceed 1×10^{11} cells per gram (Alongi, 1988). Assessments of microbial communities within burrowed sediment are similar (Steward et al., 1992), and, accordingly, burrows could be considered as loci for sedimentary microbial activity. Interestingly, Marinelli et al. (2002) demonstrated experimentally that tubes with a longer residence time were characterized by higher microbial biomass and a distinctive anaerobic signature, relative to tubes having short residence times. In their study, irrigation frequency had minor effects on the microbial community structure, suggesting instead that the properties of the burrow microenvironment, including residence time, nature of the substrate, and depth of penetration, exert fundamental controls on the microbial community in burrow linings and strongly influence biogeochemical processes within short time scales.

Unfortunately, a comprehensive geobiological model linking microbial activity with burrow distribution and diagenetic reactions remains undeveloped. In part, this is because the complex spatial distribution of biogeochemical zones is superimposed on the larger scale and heterogeneous distribution of animal burrows. For example, a patch of sediment likely contains animals that live in deep-seated domiciles (up to 2 m in depth), a range of animals living in burrows that extend 10–20 cm below the sediment-water interface, and many species that mix the upper few centimeters of sediment. Yet existing models of burrows are usually limited to solitary open burrows that simply extend geochemical zones into the sediment. Furthermore, the geobiological implications of different burrowing behaviors, such as advection, intrusion, and sediment swimming, and the interdependence of those behaviors with grain-selective and organic linings remain poorly constrained. Consequently, it is difficult to predict how the geometry and composition of such ichnological structures link with biogeochemical zonation, even though it is from this mosaic of physical and geochemical heterogeneities that many of the initial substrates for sediment diagenesis are derived.

Establishing the potential range of geobiological interactions in modern settings is also important to developing a meaningful understanding of sedimentary rocks. Such knowledge could be used to refine paleodepositional settings, with the aim being to improve stratigraphic correlations, paleogeographic maps, and models applied to resource-bearing strata (Pemberton et al. 1992). Equally important, the distribution of mineral dissolution and cementation fundamentally influence the permeability of sedimentary rocks and, hence, the resource quality in hydrocarbon-bearing strata (Pemberton and Gingras, 2005). In the rock record, we reverse model sedimentary conditions from the preserved ichnological and sedimentological features present. A typical analysis of sedimentary facies stands to infer hydraulic conditions, the composition of pore waters and the overlying water column, the influence of their mixing, and the organization of food-resource use. The results of such studies elucidate the depositional environment, while petrographic studies are commonly used to decipher facies analysis. Dissolution and cementation histories, however, are described normally in terms of pore-water evolution without careful consideration of potential linkages to a dynamic microbiological community, in spite of the fact that the geochemical and mineralogical natures of cementation patterns (i.e., stable isotopes, cation distribution, crystal structure, and mineral distribution) are influenced almost certainly by burrow microenvironments and their itinerant microbial communities (e.g., see Fig. 2).

Nonetheless, our understanding of sediment biogeochemistry and the intricate subtleties of animal-microbe interactions will certainly advance

FIGURE 2—Example of iron mineralization associated with burrow microenvironments in a modern tidal flat deposit, Willapa Bay, Washington State. Larger burrows are $\sim$4 mm in diameter and belong to nereid polychaetes, corresponding to Fig. 1H. Smaller burrows (<1 mm in diameter) are produced by capitellid polychaetes, corresponding to Fig. 1E.

rapidly with the advent of new geochemical and molecular techniques. The traditional means of pore-water sampling through sectioning core and centrifugation are now, when suitable, being replaced with microelectrode profiling. These glass electrodes, with tips as small as a few micrometers in diameter, make it possible to analyze the chemical environment (e.g., O_2, H_2S, H_2, pH, Eh), as well as some microbial processes, in dimensions relevant to the life of the microbial community. Nonspecific electrodes, which employ scanning voltammetry, have also proven useful for measuring Fe and Mn concentrations on small spatial scales. Such methods, for example, have revolutionized our understanding of how the hydrodynamic boundary layer and bioturbation affect the diffusion of O_2 across the sediment-water interface (e.g., Zorn et al., 2006).

Meanwhile, the use of SHRIMP (Sensitive High Resolution Ion Microprobe) and MicroCT (Microcomputed Tomography) will provide the ability to spatially resolve rock fabrics and obtain discrete geochemical assessments of individual minerals, thereby producing better interpretations of diagenetic cements at the scale required to reveal microbiological influences. Electron microscopic techniques will enable workers to ascertain the structure of microbes and mineral phases associated with burrows. In terms of the microbiology, the routine use of stable isotope probes have made it possible to distinguish in situ microbial metabolic activity (e.g., Radajewski et al., 2000), while nucleic acid probes are being used to more fully characterize community structure (e.g., Boetius et al., 2000). Just recently, Eek et al. (2007) described how carbon isotopic analysis of microbial cells could be sorted by flow cytometry, and Thiel et al. (2007) presented the use of ToF-SIMS (Time of Flight–Secondary Ion Mass Spectrometry) for the in situ analysis of specific biomarkers on a micrometer scale. Together, this collection of techniques provides an array of ways to link the identity of specific microorganisms to the geochemical processes they mediate.

Other promising developments are coming from the application of functional genomics and proteomics to assess gene expression and protein production. For example, DNA microarray technology is being used to determine how, and how rapidly, microorganisms respond to geochemical changes in their habitat (Newman and Banfield, 2002). In the near future, it might even become feasible to document the gene content of all organisms within a burrow environment and, through integration with high-resolution geochemical methods, decipher the flow of energy and elements between community members and the surrounding sediment.

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