

Bacterial surface structure, physicochemistry and geo-reactivity

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New approaches using cryo-transmission electron microscopy (cryoTEM) are providing a better understanding of the chemical and physical nature of bacterial surfaces. For example, the cryoTEM technique of freeze-substitution not only preserves well the native structure of bacteria, it also allows the decoration of surface reactive sites with heavy metal stains so that the sites can be readily visualized. Frozen thin sections, on the other hand, cannot be stained but rely on the mass distribution of biomatter to scatter electrons in the cryoTEM for imaging. Since the biomatter remains hydrated while visualized, these images show the bacterial surface in its finest natural detail. Correlation of freeze-substituted thin sections with frozen hydrated sections reveals exactly where on the surface of bacteria metal-interacting sites occur.

Combining cryoTEM with nuclear magnetic resonance analysis (NMR) and sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) of outer membrane components such as extracellular polysaccharides (EPS) and lipopolysaccharides (LPS) enables determination of the composition and distribution of polymers over the surface of gram-negative bacteria. Moreover, uniting these studies with examination of cell surface charge, ligand concentration and pK_a values, hydrophobicity and mineral adhesion enables the attachment of cells to mineral surfaces to be explained at the molecular level. This multi-faceted approach allows the heterogeneity and complexity of the cell surface to be realized, enabling improved explanation of how cell surface physico-chemical properties control cell-mineral interactions.

Interfacial free energy relationships in bacterial surface-mineral interactions

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The behavior of bacteria as geochemically reactive solids extends from the chemical reactivity of structural polymers in the walls and external sheaths or capsules around cells. Interactions arising from this reactivity between bacterial surfaces and minerals relate in thermodynamic terms to interfacial free energy (i.e., surface tension γ , the minimum work required to create a differential increment in surface area, $\gamma = \partial G / \partial A$). The link to geochemistry is forged directly by γ controls on mineral nucleation, adherence and solubility, the later of which explains the kinetic basis of the Ostwald step rule. For a mineral that forms in an aqueous medium (i.e., homogenous nucleation), the interfacial free energy is given by $\Delta G_{\text{surf}} = \gamma A$. When mineral formation takes place on the surface of a bacterial cell (i.e., heterogenous nucleation), $\Delta G_{\text{surf}} = \gamma_{\text{mw}} A_{\text{mw}} + (\gamma_{\text{mb}} - \gamma_{\text{bw}}) A_{\text{mb}}$, where subscripts refer to mineral-water, mineral-bacterial, and bacterial-water interfaces. Comparison of the size distribution of minerals that form at the same saturation state on and away from bacteria indicates that γ is reduced by cell contact. This means that the activation energy barrier that retards homogenous nucleation is reduced, making heterogeneous nucleation on bacterial cells energetically and kinetically more favorable. Another implication is that $\gamma_{\text{mb}} < \gamma_{\text{mw}}$, a condition that is consistent with surface adsorption (e.g., adherence) of minerals to bacteria as anticipated from the Gibbs equation. Once mineral precipitates have formed, or been adsorbed, on bacterial surfaces, the solubility of fine particles tends to decrease owing to reduced γ . This results in slower rates of crystal growth, effectively stabilizing small particles that would otherwise increase in size. Such events are evident in particle size distributions where mineral grains associated with bacteria tend to be smaller and exhibit less size variation than those away from cells. Another consequence is that mineral precipitation in association with bacterial cells can prevent the transformation of an otherwise less stable intermediate phase into a more stable insoluble form. These general observations concerning interfacial free energy relationships in bacterial surface-mineral interactions are consistent not only with data from laboratory and field investigations, but also the geological record of microfossil evidence documenting fine-grained mineral preservation of bacterial cells.