# TAPHONOMIC MODES IN MICROBIAL FOSSILIZATION

*Jack Farmer*
*Department of Geology*
*Arizona State University*

## Introduction

The microbial fossil record encompasses a wide variety of information (Figure 1) including morphological fossils (e.g., preserved cellular remains, microfabrics, and stromatolites) and chemofossils (e.g., organic biomarker compounds, isotopic and other geochemical signatures, including biominerals). Observations range in scale from mesoscopic biosedimentary fabrics, to microscopic cellular structures, to sub-microscopic chemical signatures. At all scales of observation, problems often arise when trying to distinguish between biological and inorganic features in the ancient rock record. Stromatolites, defined as laminated biosedimentary fabrics formed by the trapping and binding of sediments and/or precipitation of minerals by microorganisms (Walter 1977), are sometimes impossible to distinguish from finely laminated sediments formed by inorganic processes (see Grotzinger and Rothman 1996). At the cellular level, the biogenicity of Precambrian microfossils has been debated and criteria suggested for identifying pseudofossils (Schopf and Walter 1983; Buick 1984; Awramik et al. 1988). Distinguishing biominerals from their inorganic counterparts has also proven quite difficult in fossil materials, and the biological interpretation of isotopic and organic chemical evidence can also be inconclusive, especially for rocks that have undergone significant diagenesis. The challenge of establishing biogenicity in ancient materials is illustrated by recent debates over the origin of features in Martian meteorite ALH 84001 (McKay et al. 1996; see also review by Treiman 1998). The following discussion is aimed at identifying approaches that may enhance our ability to recognize biosignatures in ancient rocks.

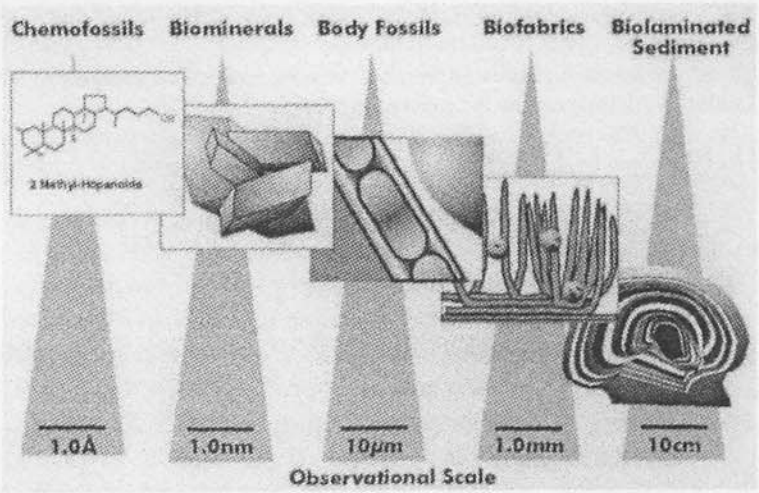


Figure 1. Types of microbial fossil information arranged from right to left in order of decreasing spatial scale.

## Importance of Spatially Integrated Studies for Assessing Biogenicity

The most important legacy of ongoing studies of the ALH 84001 meteorite may ultimately prove to be the value of the approach used, namely the integration of evidence over a broad range of observational scales. In developing integrated approaches to the study of biogenicity in ancient materials (whether of terrestrial or extraterrestrial origin), the challenge to the paleontologist is basically threefold. First is to place field samples within a well-defined geological (stratigraphic/age and paleoenvironmental) context. Although the materials may themselves contribute to such knowledge, detailed studies generally demand an understanding of both regional and local geology. Second is the detailed mesoscopic and microscopic characterization of individual samples. Establishing a detailed framework of microscopic observations is requisite for subsequent microsampling of a rock for geochemistry. This involves the identification of mineralogical and microtextural frameworks to distinguish between primary and secondary (diagenetic) features and to establish sequences of mineral paragenesis. At this step it is important to avoid sample contamination or the introduction of structural artifacts during sample preparation that can lead to misinterpretations. The third step involves the application of microsampling methods to place geochemical observations within the microscale spatial and temporal frameworks defined in Step 2. With the development of more spatially refined sampling methods it is now possible to chemically interrogate single mineral phases within rocks. This enables a much more refined understanding of the microenvironmental factors that have affected the preservation of fossil biosignatures.

Even using the spatially integrated approach outlined above, biogenic hypotheses often remain untested. The debate over ALH84001 illustrates this point. Hypothesis testing needs to be more than just confirmatory in nature. Because inorganic processes can so easily confuse biological interpretations in ancient materials, every opportunity should be taken to *disprove* life-based hypotheses. Because we are working with complex historical systems, side-by-side comparisons of modern biological and inorganic analogs may be required to adequately formulate and test hypotheses.

## Taphonomic Bias and Common Modes of Preservation

Taphonomy is that subdiscipline of paleontology that cleats with the transition of fossil remains from the biosphere to the lithosphere (Efremov 1940; Wilson 3988). Jn his review of taphonomy, Muller (1979) included a consideration of the cause of death, the processes of decomposition (necrolysis), postmortem transport or other events leading up to burial (biostratinomy) and post-burial events, inclusive of chemical and mechanical changes that occur within the sediment (fossil diagenesis). Taphonomic concepts have been developed largely with reference to multicellular organisms, but the same basic principles apply to the microbial fossil record (e.g., Bartley 1996; Knoll 1985; Knoll and Golubic 1979; Oehler 1976). In the present context, an understanding of common taphonomic modes in microbial fossilization has value in providing additional criteria for assessing biogenicity .

## Preservational Modes in Precambrian Marine and Lacustrine Environments

In Precambrian paleontology, studies of organically preserved cellular remains have provided the most complete paleobiological picture of early microbial life, However, the Precambrian record reveals a strong preservational bias based on lithology, paleoenvironment, and the structure of organic materials (Knoll 1385). Perhaps the most instructive Precambrian fossil microbiotas arc those preserved as three-dimensional forms in silica or phosphate. Figure 2A provides an example of preservation in silica from the 2.15 Ga. Belcher Island Group of Canada (Hofmann 1976; photomicrograph courtesy of Hans

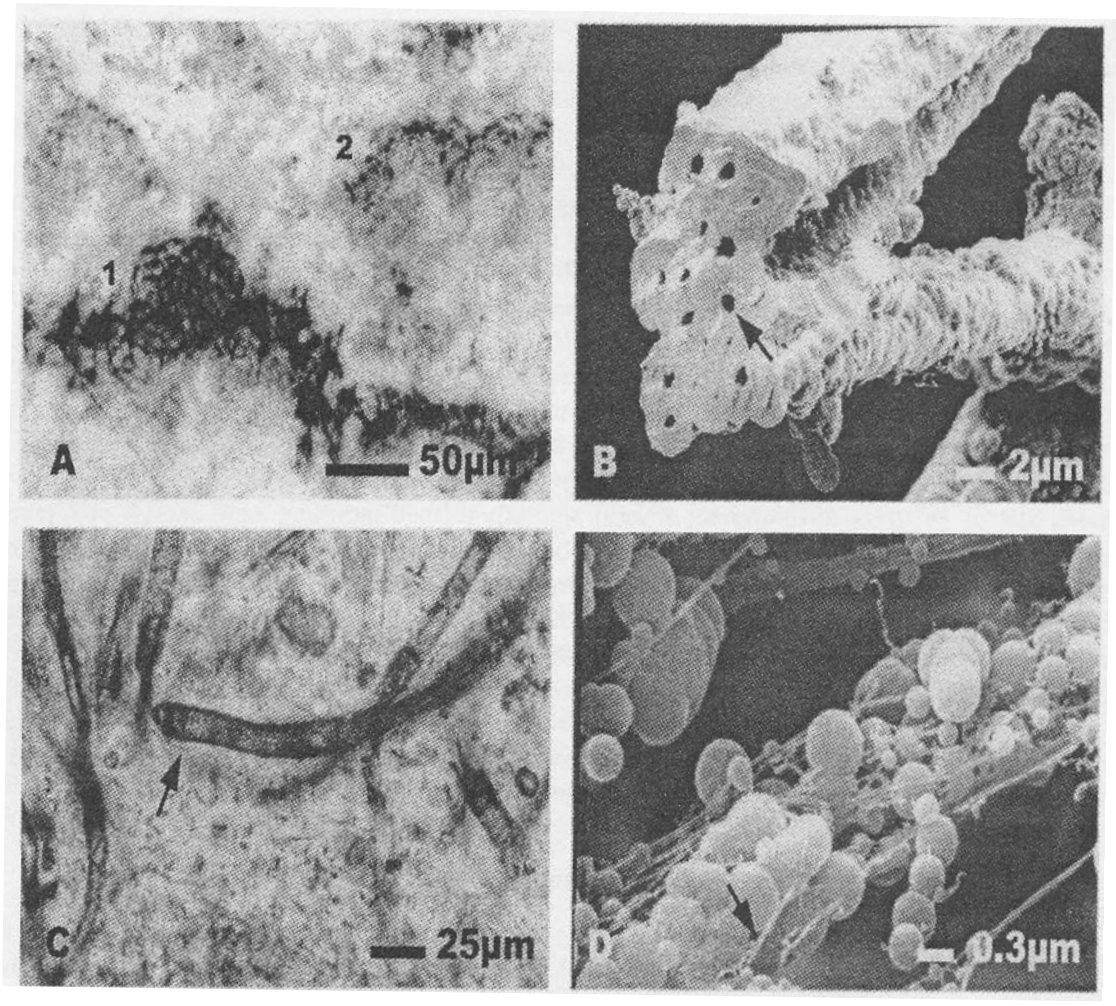


Figure 2. Common taphonomic modes. (A) Thin section photomicrograph of fossilized cyanobacterial mats dominated by a colonial coccoid species of *Eoentophysalis*. Sample from a silicified limestone of the Belcher Island Group, Canada. Early silicification of some laminae enhanced organic matter preservation (compare 1 and 2 on image). Photo courtesy of Dr. Hans J. Hofman. (B) Filament molds of *Phormidium* (filamentous cyanobacteria) formed by encrustation of trichomes. Sample from mid-temperature facies, Excelsior Geyser Basin, **Yellowstone** National **Park.** (C) **Preserved** sheaths of *Calothrix* (filamentous cyanobacteria), within a pisolith, from the Beach Geyser **Group,** Yellowstone National **Park.** (D) Critical point dried sample of a *Calothrix* mat showing **clusters** of silica **spheres** intimately interspersed within the dried filamentous remnants of an exopolymer **matrix** (see **arrow** in C).

Hofmann). In this case, silica was infused into thin mats of *Eoentophysalis,* a colonial coccaid cyanobacterium. In this **case,** the early silica permineralization **of** extracellular capsules preserved the external form of individual cells, as well as important aspects of the mat architecture (type **of** mat growth, stratification of organisms, etc.). Must Precambrian examples of this type were deposited in peritidal marine shorelines of elevated salinity (Knoll 1985). The second major **tithotype** is fine-grained, clay-rich detrital sediment (shale and volcanic ash) where microbiotas are preserved as two-dimensional compressions flattened during the compaction **of** sediments. These sediments usually represent deeper basinal settings where anaerobic conditions prevailed. Although several studies have demonstrated that rates of aerobic and anaerobic decay of organic matter do not differ significantly over a broad range of environments (see Lee 1992 and references therein), rates of early diagenetic mineralization have been shown to be higher in anaerobic environments. **Such** early mineralization **is** perhaps the most important singular factor in promoting organic matter preservation **(Allison** 1988; Allison and Briggs 1991).

## Taphonomic Trends in Siliceous Thermal Springs

**AS** illustrated by the Belcher Island example. the microbial fossil record is strongly biased toward organisms that possess degradation-resistant cell walls and extracellular envelopes (sheaths and capsules). Another example that itlustrates this point is drawn from taphonomic studies of modern and ancient siliceous spring deposits (Farmer and Des Marais 1994; Farmer et al. 1995: Jones and Renaut 1997; Jones et al. 1997; Cady and Farmer 1996; Walter el al. 1998). In rapidly **mineralizing** thermal springs, the dominant mode of preservation is encrustation of biological **surfaces** by precipitating minerals. followed by the rapid degradation of organic materials to produce external molds of cells and filamerits (Figure 2B). Occasionally, within the lowest temperature facies of thermal spring deposits, partially degraded and permineralized trichomcs are observed. But generally speaking, only the sheaths **of** cyanobacteria (which resist degradation) are preserved in sub-recent fossil materials (Figure 2C).

Comparative taphonomic studies of modern and ancient thermal spring deposits suggest that preservation is strongly skewed toward higher order biofabrics (stromatolites and biologically mediated microtextures) with cellular preservation being limited to lower temperature facies. The fidelity ***of*** cellular level preservation appears to increase with decreasing temperature, in large part owing to systematic biological changes that occur along thermal gradients. **At** temperatures below ~59°C (the upper temperature limit for thermophilic species of *Phormidium,* a *filamentous* cyanobacterium), mats typically increase in thickness, exhibiting a wider variety of surface textures and internal mat fabrics. Below ~35°C, mats similarly show **a** wide variety of mat structures preserved as stromatolitic fabrics. But in addition, over these temperatures, filamentous cyanobacteria (e.g., *Calothrix*) exhibit substantially **larger** cell diameters and much thicker sheaths, a factor that enhances cellular level preservation.

## Effects of Silica Diagenesis

During the early diagenesis of siliceous **spring** deposits, there is a pervasive structural reorganization of primary sedimentary fabrics owing to the recrystallization of metastable silica polymorphs (Opal **A)** to quartz. At the cellular level, only **the** filamentous and coccoid species having **cell** diameters larger than ~2 μm and that possess thick extracellular sheaths or capsules, survive diagenetic recrystallization. Thus, within siliceous spring deposits at all scales, the morphological fossil record is heavily biased toward the *filamentous* cyanobacteria (photoautotrophs) and, in particular, larger species that occur below temperatures of ~59°C in modern springs. The smaller coccoid and filamentous Bacteria and

Archaea (cell diameters usually <1 μm) that dominate at temperatures >73°C are also rapidly encrusted by silica. But, in the absence of thick cell walls or extracellular sheaths, entombed organic matter is rapidly decayed away, leaving behind only external molds that are rapidly infilled with opaline silica. During recrystallization there is a tendency for grain size to increase. Fine crystallites of amorphous Opal A (<5 μm; see Figure 2D) are first replaced by microquartz (5-20 μm), which are in turn replaced by megaquartz (20 to >200 μm; see Hesse 1990). This results in the loss of most primary microstructure (see Walter et al. 1998). Because of their small size, the 1-2 μm cell molds of smaller Bacteria and Archaea are quickly obliterated during recrystallization. Acid etching of ancient chert samples sometimes reveals a variety of simple spherical and rod-shaped forms within the matrix of the rock. However, at the microscale, inorganic precipitates of silica exhibit shapes very similar to simple cells, and cell-like forms may also be formed inorganically during the acid etching process, In the absence of cross sectional views that show evidence of a cellular structure, such morphological features are not compelling evidence for biogenicity.

## Microbial Biomineralization

An understanding of the varied roles that microorganisms play in mediating mineralization processes is of fundamental importance in understanding fossilization, the origin of biosedimentary fabrics. and the processes of early diagenesis. There are a potentially wide variety of processes that are of interest in this context (see Ehrlich 1996), but for convenience they may he grouped into active processes in which mineral precipitation is directly driven by the metabolic functions of an organism and passive processes in which precipitation is influenced by the structure (e.g., cation-binding) properties of cellular or extracellular materials. In the following discussion, emphasis is placed on passive processes and the importance of extracellular materials in mineralization.

### Metal-binding Capacities of Microbial Cell Walls and Extracellular Exopolymers

Natural microbial populations usually secrete large amounts of extracellular exopolymer (EPS), ranging from tightly structured capsules and sheaths around cells to a more loosely bound slime that forms the matrix of microbial biofilms and mats. Decho (19961) identified a wide variety of functions for EPS, including (1) buffering the microenvironment around cells against changes in pH, salinity, and the harmful effects of toxins (e.g., heavy metals); (2) protection against the harmful *effects* of UV radiation and desiccation during exposure; (3) protection against digestion by grazers; (4) adhesion of biofilms to surfaces; and *(5)* the concentration of exoenzymes and nutrients required for growth (including dissolved carbon compounds).

Microorganisms adsorb and concentrate many metallic cations required €or growth through electrostatic interactions with anionic carboxyl and phnsphoryl groups *in* the cell wall. In addition, however, the exopolymers that surround cells are also very reactive and can readily bind metals such as iron (Konhauser et al. 1993,1994). EPS is a highly hydrated material (~99% water) possessing an extremely porous fibrillar structure that renders it highly adsorptive. The polysaccharides of EPS possess abundant anionic carboxyl and hydroxyl groups that provide potential binding sites for metals. Of special importance arc the carboxyl groups of uronic acids (carboxylated polysaccharides) that correlate strongly with the metal binding capacity of EPS (Kaplan et al. 1987). EPS can bind a wide variety of metals, including Pb, Sr, Zn, Cd, Co, Cu, Mn, Mg, Fc, Ag, and Ni @echo 1990 and references therein). The metal binding capacity of EPS is strongly influenced by pH, being highest around pH 8 (average seawater). Preliminary studies of mineralization in siliceous thermal springs suggest that much of the

silica nucleates within the **EPS** matrix of mats over a pH range of 8 to 9 (Farmer et at. 1997; see also Figure 2D). Ferris et al. (1989) reported that near neutral pH, microbial biofilms concentrated metals up to 12 orders of magnitude higher than observed under acidic conditions. Neutral to alkaline microenvironments are commonly produced within microbial mats and biofifms through such processes as photosynthesis and sulfate reduction (Krumbein 1979).

## Biomineralization as a Factor in Microbial Biosedimentology and Fossilization

Given the ability of EPS to concentrate various metals, it is not surprising that bacteria have been implicated in a wide variety of biomineralization processes. **As** a result of cellular metabolism, microorganisms alter the chemical microenvironment around the cell, modulating the pH, as well as the concentration of a variety of organic and inorganic solutes. This can induce the large-scale precipitation of authigenic minerals in natural environments. Some cxamplcs follow.

Thompson and Ferris (1990) attributed seasonal "whilings" in Green Lake, New York, to the precipitation of calcium carbonate, gypsum, and magnesite **by** the coccoid cyanobacterium, *Synechococcus*. During photosynthesis, the pH microenvironment around individual cells becomes more alkaline owing to the extraction of $CO_2$. **This** can result in supersaturation with respect to the previously mentioned phases. Using TEM, Thompson and Ferris (1990) showed that these minerals actually nucleate on the S-layers (extracellular envelopes) surrounding cells (see Beveridge and Graham 1991 for a discussion of S-layers in bacteria). In Green **Lake,** *Synechococcus* exhibits **a** unique double S-Iayer arrangement. **As** the outer layer becomes fouled with minerals, it is shed and sinks to the bottom, accumulating on the lake floor as a fine-grained carbonate deposit (micrite). During *Synechococcus* blooms, whole cells can become encrusted **by** this process and incorporated into the sedimentary record.

Konhauser et al. (1994) found that the bacteria comprising epilithic biofilms of riverine environments sequestered significant amounts of iron, along with smaller **amounts** of Ca, K, Si, Al, and Mn. Mineralization ranged from Fe-rich EPS capsules to more extensive fine-grained mineral precipitates. Authigenic minerals ranged from complex amorphous (Fe, Al) silicates of variable composition to more silica-rich ordered phases intermediate between glauconite and kaolinite.

Zirenberg and Schiffman (1990) reported the encrustation and replacement of bacterial filaments by metal sulfide minerals and silica in deep **sea** hydrothermal vent environments. They suggested that bacterially mediated processes may contribute to the formation of base-metal sulfide deposits by concentrating silver, arsenic, and copper from seafloor hydrothermal fluids. At lower temperatures, pyrite ($FeS_2$) **is** a common mineral phase **in** fine-grained, organic-rich marine sediments. It is formed under anaerobic conditions **by** the reaction of iron-bearing detrital minerals **in** sediments and $H_2S$ produced by bacterial sulfate reduction (Canfield and Raiswell 1991).

Some of the most spectacular examples of microbial fossilization involve the permineralization of organic materials by phosphate minerals (e.g., Xiao et al. 1998). Piper and Codespoti (1975) suggested that the precipitation of carbonate fluorapatite (phosphate) in marine environments may be controlled by the bacterial denitrification of anoxic sediments at sites where the oxygen minimum zone intersects the seafloor. The **loss** of nitrogen results in a decline in microbial production and the secretion of bacterial phosphatases (see Ehrlich 1996). Such processes may govern the precipitation of phosphate minerals in seafloor sediments, thus favoring the early diagenetic mineralization and fossilization of organic materials (e.g., Rao and Nair 1988).

## Discussion

During this workshop both theoretical and empirical approaches have converged on a minimum cell diameter of between 200-300 nm €or free-living organisms. However, taphonomic (prescrvational) biases place different constraints on the lower size limit for *fossil* microbes. Comparative taphonomic studies of the Precambrian fossil record and modern analogs indicate a strong preservational bias, favoring higher order biosedimentary structures and biofabrics. In providing evidence of biogenicity, such features are often not definitive. In contrast, while providing more compelling cvidence for biogenicity, organically preserved cellular structures are also much rarer in the record. In addition, taphonomic biases favor microorganisms that are larger than a few microns in diameter and that possess thick cell walls and/or extracellular structures. This constitutes a strong taphonomic filter that excludes most smaller organisms from entering the record.

In seeking an answer to the question posed to this panel—Can we understand thc processes of fossilization and inorganic chemistry sufficiently well to differentiate fossils from thc artifacts in a sample?—the preceding examples suggest potential directions for future study. Microorganisms mediate a wide variety of natural mineralization processes. To a large cxtcnt this appears to be underpinned by the seemingly universal adaptive value of extracellular exopolymers in regulating the biology of microorganisms. The strong tendency of EPS to scavenge a wide variety of metallic cations from the surrounding environment suggests that we may improve our ability to detect hiogenic signatures in rocks by searching well-characterized samples for anomalous concentrations of trace metals. In conjunction with other types of chemofossil evidence (e.g., isotopes and organic biomarker compounds), spatial distributions of trace metals that are comparable in pattern and scale to microbial cells and biofilms may provide additional cvidence for biogenicity. And through an improved understanding of the varied role(s) played by trace elements in modern microbial processes, we may eventually be able to extract paleobiological information from rocks even where primary organic materials have been completely degraded and lost. The limiting factor is likely to be the survival of trace element biosignatures during diagenesis, a problem that can be addressed through detailed comparisons of modern and ancient analogs.

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