Microbes and volcanoes: A tale from the oceans, ophiolites, and greenstone belts

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ABSTRACT

Submarine volcanic glass alteration displays two easily discernable types of textures, one that is best interpreted as the result of an abiotic diffusive exchange process and another that involves microbial activity. Glass bioalteration textures dominate in the upper 300 m of the oceanic crust and have been found in nearly all ocean basins and in many ophiolites and greenstone belts back to 3.5 Ga. Bioalteration may involve a globally significant biomass and may influence geochemical fluxes from seafloor alteration. Glass bioalteration creates an entirely new discipline of research that involves microbiologists and volcanologists working in active volcanic systems and in the geologic record. Submarine volcanoes exposed on the ocean floor are studied along with ophiolites and greenstone belts to understand Earth not only as a physical and chemical heat engine but also as a bioreactor.

INTRODUCTION

Studies of modern and ancient volcanoes on the ocean floor as well as in ophiolites and greenstone belts tell important parts of the story of how Earth works as a "heat engine," in which planetary heat loss drives mantle convection and plate motions. Recently, these studies have shown that submarine volcanoes may host substantial biological communities that create characteristic bioalteration textures in volcanic glass (Fisk et al., 1998; Furnes et al., 2001a). These processes could play a globally significant role in terms of the distribution of biomass or mediating basalt alteration and the chemical fluxes between the oceanic crust and seawater (Furnes and Staudigel, 1999). These observations add an exciting new angle to the study of submarine volcanoes on the ocean floor, in ophiolites, and in greenstone belts.

In the spirit of interdisciplinary integration, we offer a critical review and some new data for what we consider to be some of the most intriguing evidence for microbial life inside submarine volcanoes: the bioalteration of basaltic glass. This geological, textural, and geochemical evidence for life has been found in oceanic crust of almost any age and all ocean basins and in a large number of ophiolites and greenstone belts. As for all textural evidence for life, the biogenicity of alteration textures has to be argued carefully, in the context of geochemical data and geology (Furnes et al., 2002; Staudigel and Furnes, 2004).

MICROBIAL ALTERATION OF VOLCANIC GLASS

Volcanic glass is a common quench product of lavas in submarine volcanic oceanic crust. It breaks down easily in the presence of seawater. For these reasons, glass alteration contributes more to the chemical mass balance of seafloor alteration than any other igneous phase in the extrusive oceanic crust (Staudigel and Hart, 1983).

Microscopic Textures

Bioalteration of basaltic glass was first described by Ross and Fisher (1986) and then explained by localized dissolution of glass from metabolic waste products of colonizing microbes (Thorseth et al., 1992). Subsequently, it was recognized that bioalteration is very common in submarine glass from any tectonic setting and geological age (see GSA Data Repository Table DR1¹).

It is important to contrast abiotic from biotic alteration of glass, which display unique textural characteristics (Fig. 1). Abiotic alteration of basaltic volcanic glass in a hydrous environment can be recognized by the darkening of the originally light yellow to colorless isotropic and noncrystalline glass (Fig. 1A). Glass transformation into yellow or tan palagonite or into slightly birefringent fibropalagonite always proceeds from the external surfaces toward an unaltered core in progressive alteration fronts (Fig. 1A). Palagonite defines concentric fronts that migrate inward toward the fresh interior of the glassy fragments, progressively smoothing or rounding off sharp edges of individual grains. Extensive petrographic and geochemical observations have led to a broad consensus about key processes that define abiotic alteration of glass (e.g., Stroncik and Schmincke, 2001): It is largely a diffusively controlled chemical exchange process, in which hydration progresses inward, removing various fractions of the mobile chemical inventory of the glass, adding some seawater components, and forming an array of alteration products, many of them resembling clays. These range in grain size from barely visible with the transmission electron microscope to clearly birefringent in a petrographic microscope. There is very little evidence in nature for wholesale (congruent) dissolution of glass under abiotic conditions except for the very earliest phases, before an immobile product layer has been established on exterior surfaces. Elements removed from glass typically crystallize as authigenic

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¹GSA Data Repository Item 2006215, Table DR1: Locations and ages of submarine extrusives with bioalteration, is available on the Web at www. geosociety.org/pubs/ft2006.htm. You can also obtain a copy of this item by writing to editing@geosociety.org.

Alteration Mode

Model

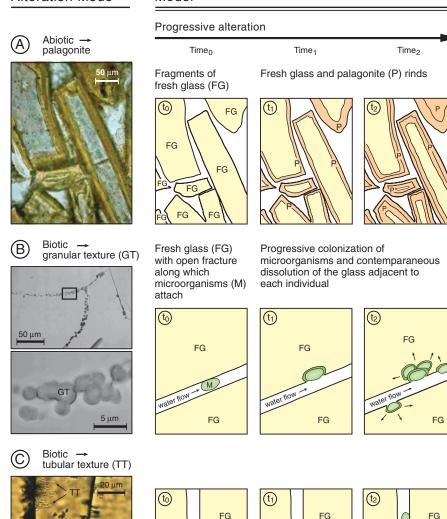


Figure 1. Thin section photomicrographs from seafloor basalts and a schematic two-step model for the development of different types of glass alteration. Unaltered fresh glass (FG) without or with microbes (green, "M") is labeled t_0 ; t_1 and t_2 are two successive stages of alteration. (A) Abiotic alteration of glass to palagonite, with fine grained grains completely altered and big grains containing some fresh cores with rounded corners. Examples for granular and tubular bioalteration are given in (B) and (C), respectively. Note the common asymmetry of tubes with respect to opposing sides. The photomicrograph in model C also contains a crack with granular alteration.

FG

FG

phases in the interstices between the glass fragments using dissolved components from the glass and from seawater (Hay and Iijima, 1968; Staudigel and Hart, 1983; Stroncik and Schmincke, 2001).

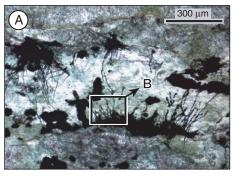
The microscopic appearance of microbially mediated glass alteration textures is quite distinct from the abiotic expression, in that alteration is reflected largely in the formation of cavities that enter the glass from exterior surfaces in granular-appearing agglomerations (Fig. 1B) or tubular (tunnel-like) morphologies (Figs. 1C and 2A–2D). In both cases, it is inferred that microbes colonize exterior surfaces or surfaces of cracks and begin to dissolve the rock through changes in pH at their contact area. The localized

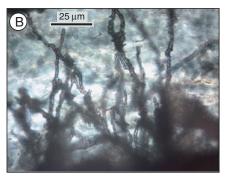
dissolution then forms these two types of bioalteration (Figs. 1B, 1C, and Fig. 2).

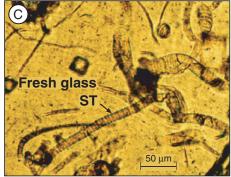
A biological origin for these features is supported by a range of textural observations:

- Bioalteration is never found completely enclosed in glass; it is always rooted on surfaces that are exposed to external water.
- Tubular and granular alteration locations on conjugate sides of a crack do not line up with one another (Fig. 1C), eliminating a preexisting weakness of the glass as a cause.
- Tube and granule diameters are of micron to submicron scale, like microbes. Tubes tend to be larger than granules, yet both display lognormal size distributions, a common attribute in biological systems (e.g., van Dover et al., 2003).
- Tubular alteration does not show flaring at the entry point or narrowing deeper inside the glass, as would be expected from abiotic dissolution.
- Some tubes show segmentation, in which the diameter of tubes varies regularly. This is highly suggestive of pulsed growth and/or the presence of several cells (Figs. 1C and 2C).
- Some tubes bifurcate, which can be explained satisfactorily by cell division.
- Some tubes show spirals (Fig. 2D)
 that are extremely hard to generate
 abiotically with the regularity
 observed. Spirals are common in
 biology and biologically produced
 materials (e.g., twisted stalks of the
 Fe-oxidizing bacterium Gallionella).
- Granular alteration often forms hemispherical agglomerations of cavities, radiating out from a single point at a crack surface and producing the texture of a sponge. These agglomerations closely resemble the growth of microbial cultures on an agar dish, except that they are three-dimensional and the medium is basaltic glass.

None of these textures can be reconciled with the diffusive model of abiotic glass alteration; a microbially mediated congruent dissolution process (Figs. 1B and 1C) is a more plausible explanation. While many details of this process remain areas of active research,







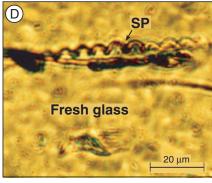


Figure 2. Tubular bioalteration textures in volcanic glass from pillow lavas and interpillow hyaloclastite. (A) Photomicrograph of thin section from interpillow sample from the Euro Basalt of the Warrawoona Group, Pilbara Craton. The tubular structures (filled with titanite) occur along fragment boundaries. The other minerals are chlorite—light green; quartz—white; calcite—brownish. (B) Detail of the titanite-filled bioalteration tubular structures. (C and D) Biogenerated structures in Cretaceous fresh glass from pillow rims, Troodos ophiolite, Cyprus, with a segmented tube (ST in C) and pronounced spiral structure (SP in D).

the biological mechanism for generating these void textures remains unchallenged even though it was proposed more than a decade ago.

The textures of bioalteration have important consequences for the development of surface area during alteration. Abiotic alteration progressively decreases surface area as grains and exposed edges are coated with non-reactive precipitates, decreasing the efficiency of diffusion as time proceeds. Biotic alteration, however, increases surface area through the creation of tubes and the "sponge-like" agglomeration of granular alteration. Staudigel and Furnes (2004) estimated a surface area increase of a factor of 2.5 for an average density of tubular alteration textures and a two orders-of-magnitude increase for granular alteration textures. While these estimates are likely bound by large errors, it is clear that surface area increases during biotic alteration, while abiotic alteration tends to decrease surface area. This indicates that dissolution becomes increasingly efficient as bioalteration proceeds, unless there is a (still to be determined) rate-limiting process that slows it down. Such a limitation could result from the lack of a particular nutrient for microbes or the inability of the system to remove dissolved components and metabolic waste products.

Geochemistry

There have been some first-order geochemical investigations of glass bioalteration, in particular studying the local geochemical environment of bioalteration textures, the fractionation of carbon isotopes during bioalteration, and water-rock chemical exchange experiments with and without the presence of microbial activity.

Elemental abundances in and around biotextures offer significant support for their biogenicity. The surfaces of cavities often contain microbial DNA (Thorseth et al., 1995; Giovannoni et al., 1996) or carbon residues and show uneven distri-

butions of biologically active elements like K, Fe, P, N, and S (e.g., Furnes et al., 2001b; Banerjee and Muehlenbachs, 2003). Alt and Mata (2000) inferred an incongruent dissolution process from the major element geochemistry of bioalteration cavities, even though any of these local geochemical effects may have occurred during or after bioalteration. Storrie-Lombardi and Fisk (2003) showed through principal component analysis that the alteration products of biotic and abiotic alteration are distinct: biotic alteration produces clays with higher Fe and K, whereas abiotic alteration produces clays with higher Mg values. This work demonstrates key differences in alteration behavior for biotic and abiotic glass alteration and sets the stage for understanding the actual processes of glass bioalteration. However, it may also be pointed out here that some of the analyses of Storrie-Lombardi and Fisk (2003) may contain secondary phases from void fillings, which suggests that some of their conclusions apply to the mineral precipitates in bioalteration cavities rather than the residual altered glass.

Carbon isotopes (δ^{13} C) show characteristic fractionation during biological processes, offering one of the most powerful tools for understanding ancient life in the rock record. Microbially produced cellular organic carbon typically is characterized by very low (i.e., negative) δ^{13} C values. In fact, bulk isotopic analysis of finely disseminated carbonate in glassy margins with bioalteration textures commonly records lower δ^{13} C than for the more crystalline interiors of the same pillows (-23 to -3 versus -7 to +5; Furnes et al., 2001b, 2005; Banerjee and Muehlenbachs, 2003; Furnes and Muehlenbachs, 2003). An opposing trend, however, could be expected from the activity of methanogenic microbes that utilize H, formed during serpentinization and seawater CO2 to produce methane with extremely light carbon. The methane escapes the system, leaving behind relatively heavy residual carbon contained in the microbial biomass or its oxidation products. Thus, light δ^{13} C values in carbonates from bioaltered glassy margins rule out methanogenesis as a major process for glass bioalteration.

Microbial activity may also have a profound impact on processes and chemical fluxes during water-rock interaction; the first experimental investigations revealed some profound differences between biotic and abiotic processes. Glass alteration experiments using surface seawater including microbes and sterile controls show substantial differences (Staudigel et al., 1998, 2004): Microbial activity enhances chemical exchange in water-rock reactions (specifically for Sr) and results in higher rates of authigenic mineral production, and it increases the uptake of Ca. Abiotic alteration results in pronounced uptake of Mg and effective removal of Si. Biotic experiments with a natural seawater microbial inoculum at temperatures up to 100 °C showed significant mobility of K, Rb, Cs, Li, B, U, Th, and Pb, where U-Pb fractionation appears to be strongly temperature dependent. While more experiments are needed to explore the biotic and abiotic controls of these processes, first order results show that microbes do have a pronounced effect on glass alteration and that some elements are particularly mobile.

Finding such differences in chemical redistribution patterns from biotic or abiotic water-rock interaction suggests that hydrothermal exchange between seawater and basalt may be different for these two modes of seafloor weathering. This implies that the chemical fluxes from water-rock interaction may have systematically changed as Earth evolved from a pre-biotic state into its present state of biological diversity and total biomass.

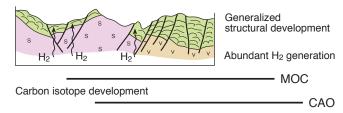
The Geological Context

The geological context and the associated geochemical and mineralogical boundary conditions are very important for the understanding of glass bioalteration.

Bioalteration of glass has been found in any submarine volcanic setting that preserves fresh (or minimally altered) glass, in fast- and slow-spreading crust and ophiolites, in oceanic plateaus, and in greenstone belts of nearly all ages (Table DR1; see footnote 1). In particular, seafloor spreading environments with dramatically different spreading rates offer different boundary conditions for bioalteration, especially with respect to the expected depth of water circulation and the composition of materials in the upper part of the oceanic crust (e.g., Dilek et al., 1998) (Fig. 3). Slow-spreading ridges (e.g., <2.5 cm/yr) show deep-rooted normal faulting that facilitates deep circulation of hydrothermal solutions, and they commonly show exposure of ultramafic rocks (Karson, 1998). At intermediate- to fast-spreading ridges (e.g., ~6-12 cm/yr), ocean crust is more likely to produce thick extrusive sections, without major tectonic disruption (e.g., Sinton and Detrick, 1992).

In order to explore the potential for such differences, Furnes et al. (2006) compared the δ^{13} C variations in bioaltered pillow margins from different ocean basins. The δ^{13} C of finely disseminated carbonates from bioaltered glassy basaltic pillow rims from slow- and intermediate-spreading oceanic crust of the central Atlantic Ocean ranges from -17% to +3% (PDB), whereas those from the faster spreading Costa Rica Rift define a much narrower range and cluster at lighter values between -17% and -7% (Fig. 3). Some ophiolites show a similar δ^{13} C variation; the Jurassic Mirdita ophiolite (Albania) shows a structural architecture similar to that of the slow-spreading central

A. Slow spreading



B. Intermediate to fast spreading

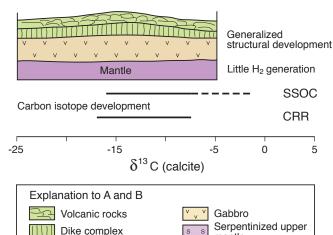


Figure 3. Inferred relationships between the structural development of oceanic crust and carbon isotope signatures. (A) Slow spreading, and (B) intermediate to fast spreading. MOC—Mirdita Ophiolite Complex, Albania; CAO—central Atlantic Ocean; SSOC—Solund-Stavfjord Ophiolite Complex, west Norway; CRR—Costa Rica Rift. Modified from Furnes et al. (2006).

Atlantic Ocean crust and a similar range in $\delta^{13}C$ values of biogenic carbonates (Fig. 3). The Late Ordovician intermediate-spreading Solund-Stavfjord Ophiolite Complex (western Norway) also displays $\delta^{13}C$ signatures in biogenic carbonates similar to those of the Costa Rica Rift (Furnes et al., 2001b) (Fig. 3). These initial results lead us to speculate about the involvement of H_2 or inorganic methane produced during the serpentinization of shallow ultramafics. This process would be particularly common at slow-spreading ridges and would ultimately lead to the relative enrichment of heavy carbon in the oceanic crust, but details of these processes remain to be explored.

The local geological and hydrological context of bioalteration can provide clues about its environmental controls, such as the exposure to circulating seawater, effective water:rock ratios, temperature, and composition and/or oxygenation of hydrothermal solutions at the time of alteration. Detailed correlations between local geology and bioalteration were made at ocean drilling sites 417 and 418 in the western Atlantic and at sites 504 and 896 at the Costa Rica Rift. Furnes and Staudigel (1999) and Furnes et al. (2001a) made quantitative estimates of bioalteration throughout these sites and compared them with a range of geological context observations. In Figure 4, we have replotted the total bioalteration estimates of Furnes and Staudigel (1999), separately for tubular and for granular alteration

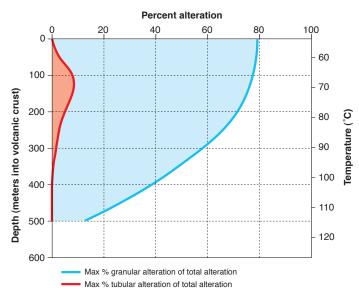


Figure 4. Depth distribution of tubular and granular microbial alteration structures (replotted from Furnes and Staudigel, 1999).

(only totals reported originally), as well as for the downhole temperature measurements at site 504. Several observations can be made in Figure 4:

- The top of the oceanic crust, an environment that is closest to the ocean biosphere, displays only minor amounts of tubular bioalteration. This trend is confirmed by studies of dredged rocks that, so far, have yielded almost no evidence of this style of bioalteration, except for some heavily Mn-encrusted pillows from old seamounts (M. Fisk, 2006, personal commun.).
- The combined tubular and granular alteration features make up ~80% of the glass alteration in the upper 300 m of the oceanic crust, suggesting that microbes are most active in this depth range.
- Overall, tubular alteration makes up a much smaller fraction of the alteration, and it shows a clear maximum at 120 m depth and the current borehole temperature of 70 °C.
- Granular alteration is the dominant form of bioalteration at all depths.

In addition, Furnes and Staudigel (1999) pointed out that the abundance of bioalteration in these sites is also correlated with the abundance of volcaniclastics, high permeability, and secondary minerals that are indicative of a relatively oxygenated environment in the upper part of the oceanic crust.

These observations suggest that optimum conditions for biotexture formation can be found at ocean crustal depths that are intermediate between the extremely high water:rock ratios at the top of the ocean floor and the more limited water circulation at depths >500 m. Bioalteration textures on the seafloor are most abundant in a temperature range between 20 and 80 °C (Furnes and Staudigel, 1999) and in the presence of more oxygenated fluids. The high abundance of biotextures is likely to imply optimum growth conditions for the responsible microbes.

8

Bioalteration textures have been found in submarine volcanoes of all ages, as old as the oldest preserved fossils on Earth (Table DR1; see footnote 1). It is important to note, however, that the ages of the host rocks do not necessarily provide an age for the bioalteration because bioalteration textures are cavities that, in principle, could be formed by dissolution any time after the initial quenching of the glass. However, bioalteration cavities in fresh glass may contain mineral precipitates from microbial activity or from later diagenetic or metamorphic reactions. Such minerals offer some help in determining a minimum age for cavity formation. One such mineral, titanite, has been found to replace tubular glass alteration features in the Barberton Greenstone Belt (South Africa: Furnes et al., 2004; Banerjee et al., 2006) and in the Pilbara Craton (NW Australia; Figs. 2A and 2B). Titanite has been found in bioalteration tubes in fresh glass in minimally (zeolite facies) altered pillow basalts from the Mirdita ophiolite (Furnes and Muehlenbachs, 2003). and it is a metamorphic mineral common to greenschist and amphibolite facies in submarine basalts. Furnes et al. (2004) pointed out that the titanite in bioalteration tubes in the Barberton belt is likely to have formed during or prior to a well-dated metamorphic event. They pointed out that the uncertainties of igneous and metamorphic ages overlap and therefore demonstrate that bioalteration textures were formed within a few million years of the eruption of the pillow lavas.

DISCUSSION

Impact of Glass Bioalteration

From a geological perspective, the impact of glass bioalteration may be substantial. So far, almost any deep ocean crustal drill hole has yielded bioalteration features in well-preserved glassy margins, independent of the age of the crust. Optimum growth conditions for (glass-bioalteration—) microbes in submarine volcanoes appear to be within the upper 300 m of the oceanic crust and at temperatures between 20 and 80 °C (Furnes and Staudigel, 1999). Such conditions are likely to be found in a substantial depth range of ocean crust, covering ~60% of Earth's surface area and occupying a very large volume of crust.

Glass bioalteration may have substantial effects on global geochemical fluxes because bioalteration is pervasive in the upper oceanic crust throughout the oceans and throughout geological history. In well-studied examples, ~75% of glass alteration in the upper 300 m is microbially mediated (Furnes and Staudigel, 1999). We know from experiments and microscale chemical analyses that microbially mediated glass alteration affects the abundances of K, Rb, Cs, U, H, and C and the isotopic ratios of Sr, O, and C (Staudigel et al., 2004). Seafloor alteration has been shown to buffer the composition of many of the elements in seawater. This raises the possibility that microbial activity may also influence the geochemical mass balance between the oceans and the oceanic crust. The recycling of the bioaltered oceanic crust deep into the mantle provides for a geochemical pathway between Earth's biosphere, hydrosphere, and mantle.

The impact of bioalteration on total carbon fixation or total biomass, however, remains elusive. Bach and Edwards (2003) estimated that submarine basalt can provide enough energy to

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support a primary production of $\sim 10^{12}$ g/yr cellular C, providing an upper limit for chemosynthetic carbon fixation in the oceanic crust. However, while we can only speculate about the biomass and the primary productivity in the deep ocean crustal biosphere, the impact may be substantial in terms of its abundance in the geological record and the geochemical fluxes between seawater, the ocean crust, and Earth's mantle.

Early Life and the Evolution of Glass Bioalteration

Glass bioalteration is among the oldest fossilized evidence for life on Earth, and its textural expressions have remained remarkably similar through geological history. The oldest evidence for glass bioalteration was found in the Pilbara (Figs. 2A and 2B) and Barberton greenstone belts (Furnes et al., 2004; Banerjee et al., 2006), next to the oldest and most primitive forms of microbial life reported from cherts in the same regions (e.g., Westall et al., 2001). Previous evidence for life around submarine volcanoes came from the 3.2 Ga filamentous microfossils in volcanogenic massive sulfide deposits (Nisbet, 2000), suggesting that life has taken a solid footing in hydrothermal vent areas. However, it is quite possible that microbial activity in the oceanic crust may have started well before 3.5 Ga, because a 300-500-m-thick deep ocean crustal biosphere may have provided some protection from early bombardment. For lack of well-preserved fossils, however, the earliest arrival of bioalteration or microbial activity in submarine volcanoes remains unknown.

The association of bioalteration with the earliest life begs the question of what role submarine volcanoes played during the origin of life itself. This role may include the interior of volcanoes as the primary environment where life originated or as a secondary environment where life found shelter or codeveloped with other settings. In either case, the study of early life in submarine volcanoes holds much promise for understanding the origin of life and its environments. Such research is aided by the fact that submarine volcanics offer a rather well-constrained setting, where the geological, chemical, and physical boundary conditions are rather obvious or at least relatively easily reconstructed with confidence.

CONCLUSIONS

Exploring the interaction between microbes and submarine volcanoes has revealed exciting discoveries but also raised many questions. Discoveries include the depth and connectedness of biosphere, hydrosphere, and lithosphere; the abundance and pervasive nature of microbial glass alteration in submarine volcanoes; and its likely impact on global biomass and biogeochemical fluxes possibly reaching deep into Earth's mantle through subduction. At the same time, there is much uncertainty about many first-order questions about how the deep ocean crustal biosphere works and the consequences of its presence. For example, we still have not isolated any microbes that can be directly related to the formation of tubular alteration. Consequently, we do not understand the nature of these consortia and what controls their function and productivity. We need to quantify chemical fluxes involved in bioalteration and observe how these microbial communities and their geochemical impact evolved through geological time.

Much of the most urgent scientific inquiries require designated biological and geochemical work in active systems, but they also require substantial efforts in studying the geological record. Without the latter, we will never understand the evolution of microbial activity through geological time and its impacts on global geochemical fractionation. This offers powerful reasons for revisiting ophiolites and greenstone belts that have been so yielding toward the understanding of the planet as a physical and chemical heat engine. Science is now focusing on understanding Earth as a bioreactor, and once again submarine volcanoes are key players in the tale of how Earth works with an interconnected biosphere, hydrosphere, and lithosphere.

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