Candidate microbial ichnofossils in continental basaltic tuffs of central Oregon, USA: Expanding the record of endolithic microborings

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ABSTRACT

The presence of potential microbial trace fossils (endolithic microborings) has been well documented in oceanic basaltic pillow lavas, hyaloclastites, tuffs, and transitional subglacial marine lavas in the past 30 yr. Despite their evident abundance in oceanic to subglacial environments, they have not been observed in continental basalts that were not erupted in marine or subglacial settings. To expand the record of putative endolithic microborings in volcanic rocks to nonmarine, continental lacustrine environments, we examined hydrovolcanic pyroclastic deposits in the Fort Rock volcanic field, central Oregon. This study presents the textures, mineralogy, and geochemistry of basaltic tuffs containing possible endolithic microborings comparable in morphology, size, and distribution to those described in earlier oceanic and subglacial basalt studies. We observed a variety of tubular and granular textures that show evidence of biogenic morphologies and behavior, and a primary geological context that expresses their age and syngenicity. Petrographic relationships with secondary phases (chalcedony, nontronite, calcite) indicate that the construction of microtunnels occurred in saline, alkaline fluids at temperatures of 25–80 °C. In addition, positive correlations were observed between the extent of aqueous alteration (fluid flux and that of those fluids may have had a direct influence on the formation process or possibly the resulting change in chemical composition of those fluids may have had a direct influence on the formation process or possibly the type of constructing microbe. This work adds to understanding of factors controlling microtunnel formation and is the first ac-

INTRODUCTION

Over the last few decades, various studies have presented evidence that submarine volcanic rocks from the upper oceanic crust, such as pillow lavas and glassy volcanic breccias (hyaloclastites), can host endolithic microbial communities (Thorseth et al., 1995, 2001; Giovannoni et al., 1996; Lysnes et al., 2004; Mason et al., 2007). The most widespread evidence cited is the distinctive granular and tubular textures thought to be produced during the processes of bioerosion, whereby microbes (euendoliths) etch volcanic glass surfaces and actively bore into the substrates (Thorseth et al., 1995, 2001, 2003; Furnes et al., 1996, 2001, 2005, 2007a, 2007b; Furnes and Staudigel, 1999; Fisk et al., 1998a, 2003; Banerjee and Muehlenbachs, 2003, 2011; Torsvik et al., 1998, 2008). Such textures appear to record the boring behavior of microbes and thus may be considered trace fossil sils (endolithic microborings).

The tubular form consists of elongate, straight, curved, spiral, or branched tunnels in fresh glass that are 1–5 µm in diameter and 10–200 µm in length (e.g., Furnes et al., 2001; Fisk and McLoughlin, 2013). The granular form is characterized by radiating clusters of spheroidal-shaped cavities with diameters of ~0.4 µm (e.g., McLoughlin et al., 2007; Staudigel et al., 2008). Granular textures tend to be more common, although tubular varieties are more easily identified because they are usually larger in size and are morphologically distinct from abiotic alteration (Furnes and Staudigel, 1999). Typically, the tubular and granular textures are hosted within fresh volcanic glass and originate along fractures, pillow rims, or volcaniclast margins. Tubules and granules may be hollow or preserved with infillings of secondary minerals such as phyllosilicates, zeolites, iron-oxide hydroxides, or titanite (e.g., Benzerara et al., 2007; Staudigel et al., 2008; Izawa et al., 2010; McLoughlin et al., 2010).

Comparable textures have also been described in hyaloclastites erupted in subglacial environments of Iceland and Antarctica (e.g., Cockell et al., 2009a; Cousins et al., 2009), as well as marine tuffs of Ontong Java (Banerjee and Muehlenbachs, 2003). The record of continental endoliths within volcanic rocks, however, is not so extensive. Although the first description of volcanic glass etching came from a nonmarine tuff layer in the Miocene John Day Formation, eastern Oregon (Ross and Fisher, 1986), they are surface features and do not penetrate far into the glass. Referred to as “biogenic grooving,” they are in the form of semicircular and U-shaped grooves with much larger widths (4–20 µm) than tube diameters described in oceanic basalts. Evidence of endolithic microbes has also been documented in continental pyroclastic rocks such as the Rattlesnake Tuff in Oregon, a high-silica rhyolite ignimbrite (e.g., Fisk et al., 1998b), and in lava flows such as the Columbia River basalts (e.g., McKinley et al., 2000) in the form of biofilms with rod-shaped microbially colonized glassy shard surfaces, and bacteriomorphs of fossilized microbes, respectively. Likewise, no textures resembling tubular or granular bioalteration have been described in these locations.

The Fort Rock volcanic field in central Oregon, United States (Fig. 1), also known as the Fort Rock–Christmas Valley basin, is the site of an ancient Pliocene–Pleistocene pluvial lake basin and over 40 hydrovolcanoes (Heiken, 1971). These features include maars, tuff rings, and tuff cones consisting of layered basaltic tuffs. The Fort Rock volcanic field also possesses geological, environmental, and chemical characteristics that are analogous to various locations on the Martian surface, including Gale Crater, the Mars Science Laboratory study site.
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Geological Society of America Bulletin, v. 128, no. 7/8, 1271

(Squyres et al., 2007; Yen et al., 2008; Schmidt et al., 2009; Bish et al., 2013; Grotzinger et al., 2014; McLennan et al., 2014; Vaniman et al., 2014). Several of the deposits throughout the Fort Rock volcanic field have been studied over the last few decades for various reasons (e.g., Hampton, 1964; Lorenz, 1970; Heiken, 1971; Colbath and Steele, 1982; Martin et al., 2005; Brand and Clarke, 2009), yet no reputed tubular and granular microborings have been described in any deposit within the basin until now.

We here present the first account of putative endolithic microborings from continental, non-marine, non-subglacial, basaltic hydrovolcanic pyroclastic deposits (Reed Rock and South Reed Rock; Fig. 1) in the Fort Rock volcanic field. Geochemical data and petrographic observations of mineralogical and textural characteristics, including abiotic palagonitic alteration and fluid conditions, are examined. We also describe the range in morphologies of putative bioalteration textures found within glassy pyroclasts, make a case for biogenicity, and attempt to define the paleoenvironmental characteristics, including temperature of formation. The term putative bioalteration is used to jointly refer to both tubular and granular textures, whereas the term microtunnel or tunnel refers only to the tubular type.

Geologic Setting

The Fort Rock volcanic field (Fig. 1) is ~40 km wide and 64 km long (Heiken, 1971). Series of NW-trending faults crosscut the basin and the surrounding highlands (Heiken, 1971) and provided pathways for ascending dikes, as indicated by lineaments of vents in the same orientation. The faults also provided pathways

Figure 1. Fort Rock volcanic field (FRVF; modified from Heiken, 1971) and Reed Rock (RR)–South Reed Rock (SRR) study area collectively referred to as Reed Rocks. Upper-left inset shows the state of Oregon (U.S.A.) with the Fort Rock volcanic field shaded in gray. Shaded area is enlarged in the upper-right panel, showing the Fort Rock volcanic field, with the location of the Reed Rock and South Reed Rock tuff rings indicated (outlined by box, labeled with an arrow) relative to lava fields and other hydrovolcanic edifices and cinder cones within the basin. The highstand lake boundary is also indicated (blue dashed line) showing that Reed Rock and South Reed Rock are located just outside of the inferred lake margin. Lower panel shows an enlarged geologic map of the Reed Rocks study area. Larger unit in northern half of map is Reed Rock; smaller unit in southern half of map is South Reed Rock (topographic base from U.S. Geological Survey, 2011).
for groundwater and allowed for hydrovolcanic eruptions to occur outside the inferred lake margin. Reed Rock and South Reed Rock tuff rings, which from here on will be collectively referred to as Reed Rocks, unless specified, are the undated pyroclastic remains of two adjacent Pliocene–Pleistocene (~2.59 Ma to 12 ka; Heiken, 1971) hydrovolcanoes in the central area of the basin ~2.5 km beyond the inferred paleolake margin. The phreatomagmatic-hydrovolcanic eruptions were therefore more likely driven by groundwater and/or shallow surface water. Although no absolute ages have been determined, the majority of samples contain relatively high proportions (37%–52%) of fresh glass. This may suggest a relatively younger mid- to late Pleistocene age.

The Reed Rocks are composed of multiple fine to coarse ash and lapilli-rich layers ranging from ~1 cm laminated to meter-scale massive quaquaversal tuffs typical of hydro- phreatomagmatic-hydrovolcanism. The blocky, angular morphologies of fine to coarse ash and lapilli basaltic glass (sideromelane) pyroclasts (Fig. 2) are typical of brittle chilling fragmentation during phreatomagmatic eruption. Tuff samples are more commonly clast supported and 3%–12% vesicular, often amygdaloidal, with connecting fracture networks resulting from explosive shattering and thermal contraction upon cooling. Rapid quenching is also indicated by swallow tail, skeletal, and sieved plagioclase, hopper olivine phenocrysts, and undercooling textures of fine-grained intergrown plagioclase and pyroxene. Bomb sags, vesiculated matrices, and scoriaceous accretionary lapilli (armored lapilli) suggest deposits saturated with up to 15%–20% external water contents (Heiken, 1971). Accidental lithic blocks up to ~1 m in diameter and very coarse angular blocks of explosion breccia lensoidal interbeds are also consistent with groundwater interaction. Reed Rock has a final lava cap (lava lake) and dike intrusion that represent the transition to effusive volcanism when the external water source was blocked from entering the vent near the end of the eruption (Heiken, 1971).

Postdepositional alteration, including both low-temperature hydrothermal alteration of mainly juvenile basaltic glass and the precipitation of ancillary precipitates within vesicles (amygdules) and voids (vugs) produced secondary textures and an assemblage of amorphous to protocrystalline and wholly crystalline mineral phases. Aqueous alteration resulted in the formation of palagonite. The palagonitization process involves a low- to high-temperature progressive aging from light-yellow amorphous (isotropic) to dark-yellow or orange-brown crystalline (anisotropic) material. Palagonitization proceeds by hydration, chemical exchange, and congruent and incongruent dissolution of basaltic glass, with accompanying precipitation of secondary phases that may include phyllosilicates, zeolites, or iron-oxy-hydroxides (Peacock, 1926; Zhou and Fyfe, 1989; Thorseth et al., 1991; Stroncik and Schmincke, 2001). The distinction suggested by Peacock (1926) between the amorphous gel-palagonite and proto- to wholly crystalline fibro-palagonite varieties is accepted. This alteration occurred where rock surfaces were exposed to circulating fluids such as along fractures, in vesicles, and on pyroclast margins.

**Pluvial Fort Rock Lake**

Considering the geologic and hydrologic similarities of Fort Rock Lake with modern western U.S. pluvial lakes such as Summer and Abert Lakes, it is likely that the Fort Rock Lake evolved through a similar evaporitic trend (e.g., Hardie and Eugster, 1970). The Pliocene Pettus Lake Member of the Fort Rock Formation, which probably underlies the majority of the Fort Rock basin, includes diatomite beds (Hampton, 1964; Allison, 1966, 1979; Heiken, 1971) with diatom associations typical of a freshwater environment (e.g., Colbath and Steele, 1982). In addition, abundant centric diatom genera have been interpreted to indicate an oligotrophic or nutrient-poor lake (e.g., Stockner and Benson, 1967). In the Fossil Lake area, located in the east-central part of the Fort Rock–Christmas Valley basin (Fig. 1), rare earth element (REE) compositions of vertebrate fossils (ca. 646 ka to 23.2 ka; mid- to late Pleistocene) have suggested that lake waters evolved from neutral pH to increasingly more alkaline saline conditions (Martin et al., 2005). By analogy, Fort Rock Lake may have also evolved from an early freshwater environment to more alkaline and saline conditions. The phreatomagmatic eruptions of Reed Rocks likely involved saline and basic external groundwater and/or lake water that was more akin to marine than freshwater conditions. In order to further constrain conditions of basalt alteration (temperature, pH), we compare the Reed Rocks alteration assemblage to examples from marine environments, such as Surtsey, Iceland (e.g., Apps, 1983; Chipera and Apps, 2001).

**MATERIALS AND ANALYTICAL METHODS**

**Sample Collection**

As part of a regional study of the Fort Rock volcanic field, representative samples of basaltic tuff, lava, and intrusives were collected from two adjacent tuff rings. In total, 16 samples (3 tuff, 3 lava) were collected from Reed Rock and South Reed Rock. The goal in sample collection was to obtain a suite that displayed a range of textures from fresh to highly altered. Obvious color differences, bedding thickness variations from laminated to massive, grain size variations, and ancillary precipitate contents were key considerations.
Petrographic Analysis

Petrographic analyses and scanning electron microscopy (SEM) of basaltic tuffs were performed to characterize primary and alteration textures, including both aqueous (abiotic) and reputed bioalteration textures. To describe the various morphologies of tubular and granular textures in comparison to those reported in oceanic basalts, we apply the terminology of Fisk and McLoughlin (2013).

Estimations of modal percentages were obtained by point counting (300–400 points per thin section). In order to approximate the relative quantity of potential bioalteration, a two-step method was applied. During point counting, the presence or absence of putative microborings within the field of view was recorded for each point to assess whether possible bioalteration was found throughout the sample, or only in a few isolated pyroclasts. Then, a method similar to that devised by Cousins et al. (2009) was adopted, whereby the proportion of possible bioalteration found along available alteration boundaries, such as pyroclast margins, fractures, and vesicles, was visually approximated in each thin section. Each was given a “bioalteration value” ranging from 0 to 10, representing no boundaries affected by bioalteration to all boundaries affected by bioalteration, respectively. To determine the abundance of the tubular morphological type in each sample, photomicrographs were used. Each micrograph was visually examined, and the presence or absence of each morphotype was recorded with a tally. These values were then used to calculate proportions. Other quantitative data obtained through point counts were compared to bioalteration values to determine whether any relationships existed with other textural features. Tunnel diameters and lengths were measured using the cellSens Standard and ImageJ software measurement tools.

For SEM observations, samples were carbon coated and analyzed using a Hitachi SU6600 at the Zircon and Accessory Phase Laboratory (ZAPLab) at the University of Western Ontario.

Mineralogical and Geochemical Analyses

Micro-X-ray diffraction (µXRD) was performed on cut rock slabs and polished thin sections using the Bruker D8 Discover Diffractometer at the University of Western Ontario. The diffractometer was operated with CoKα radiation (λ = 1.7898 Å) generated at 35 kV accelerating voltage and 45 mA beam current with a Co Gobel mirror parallel optics system having 0-0 geometry. Use of 100 µm or 300 µm nominal beam diameters permitted in situ analysis at the microscopic scale and enabled correlation between crystal structural data and other microscopic data such as polarizing microscope observations (Flemming, 2007). The µXRD data were collected on a two-dimensional (2-D) general area detector (GADDS) and integrated to generate a conventional intensity versus 2θ diffraction pattern for mineral identification using the International Center for Diffraction Data (ICDD) database. Powder X-ray diffraction was also performed on bulk samples with a Rigaku D/MAX diffractometer. Lava samples were sent to the Washington State University (WSU) GeoAnalytical Laboratory to determine elemental compositions using a ThermoArlAdvantXP+ sequential X-ray fluorescence (XRF) spectrometer. Energy dispersive spectrometry (EDS) was used for microchemical elemental analysis.

RESULTS AND DISCUSSION

XRF Results

Major-element concentrations are markedly similar between the three lava-intrusive samples, with ranges of 50.02–50.08 wt% SiO₂, 8.36–8.47 wt% total Fe as FeO*, and Mg# = 67, where Mg# is defined as molar 100MgO/(MgO + FeO). The lavas are low in K₂O (0.36–0.39 wt%), consistent with a petrographic classification as low-potassium tholeiitic basalts, an incompatible element–poor basalt type common in the Fort Rock volcanic field (Jordan et al., 2004).

X-Ray Diffraction and Petrography

X-ray diffraction patterns of the glassy tuffs are typified by a broad elevated area (or “amorphous hump”) at ~15°–40° 2θ (Figs. 3B and 3D). Igneous minerals identified include plagioclase, olivine (Fig. 3A), pyroxene, and oxides. Secondary minerals include the zeolite chabazite with lesser phillipsite, the smectites nontronite (Figs. 3B and 3C) and saponite, and calcite (Fig. 3D). Chabazite infills vesicles and voids and comprises part of palagonitic alteration. A typical pattern is depicted in Figures 3B and 3C. The more common and pervasive amygdaolidal and vug calcite exhibits the most distinct diffraction pattern (Fig. 3D), with fine radial dendritic or bladed to granular or massive habits. Nontronitic smectite is identified in areas with yellow palagonitic alteration, and 2d spacings are consistent with some interlayered saponite. Palagonite rim coatings range from 5 to 30 µm in thickness propagate inward as alteration fronts progress toward unaltered glass, many clasts of which have unaltered cores with only exterior alteration rims (e.g., Fig. 4A). Most completely palagonitized clasts are of fine and coarse ash sizes. The amorphous gel-palagonite form is most common, but the protocrystalline fibro-palagonite form is present in minor quantities (Table 1).

Considering the secondary phase assemblage, the specific temperature and pH conditions in which they have been documented to form, and their petrographic relationships, an approximation of the hydrothermal alteration conditions within the Reed Rocks basaltic tuffs may be made. We note that the processes by which zeolites and palagonite form are complex and not fully understood, and we acknowledge that these interpretations are based on observation and previous studies.

Formation of Chabazite (Zeolites)

If the Fort Rock Lake waters were fresh during the late Pliocene (Colbath and Steele, 1982) and became more saline and alkaline during the mid- to late Pleistocene (Martin et al., 2005), then the existence of amygdaolidal chabazite (Figs. 3B, 3C, and 5) is consistent with Reed Rocks having erupted in the mid- to late Pleistocene into saline-alkaline waters. Chabazite forms most stably in saline-alkaline (pH 9–10) water in lake environments and in cavities of mafic rocks as a result of hydrothermal fluids (Kristmannsdóttir and Tómasson, 1978; Chipera and Apps, 2001; Utada, 2001). The formation of chabazite is also most stable in the low-temperature regime below 100 °C (Chipera and Apps, 2001). The approximate temperature range for the formation of chabazite in Icelandic geothermal deposits is for example ~10–80 °C (Apps, 1983; Chipera and Apps, 2001). This is therefore considered to be the temperature range of zeolite formation within the Reed Rocks tuffs.

Formation of Calcite

The abundance of calcite (0%–15%) is also strongly indicative of neutral to alkaline fluids (Chipera and Apps, 2001; Chevrier et al., 2007). Calcite forms over a much wider temperature range (0–270 °C) than chabazite (Apps, 1983) with more variable habits. Calcite at Reed Rocks likely precipitated throughout hydrothermalism and diagenesis. Zoned amygdules in palagonitized clasts are observed where vesicle surfaces are coated by zeolites and infilled with calcite (Fig. 5). These amygdules suggest that calcite continued to precipitate after palagonitization was complete, as well as after zeolite formation at temperatures below 80 °C (the upper temperature limit of chabazite stability; Apps, 1983).
Formation of Nontronite Smectite and Palagonite

Nontronite smectite is a primary component of palagonite (e.g., Eggleton and Keller, 1982; Staudigel and Hart, 1983; Stroncik and Schmincke, 2001). The lower temperature limit of smectite (nontronite) formation is interpreted to be ~25 °C (Jakobsson and Moore, 1986; Chipera and Apps, 2001). Under hydrothermal conditions (>120 ± 5 °C), palagonitization is complete, and olivine alters to smectite (nontronite and saponite; Jakobsson and Moore, 1986). Because olivine at Reed Rocks is unaltered, hydrothermal temperatures likely did not reach 120 °C. In hydrothermally altered Icelandic basalts, Apps (1983) found palagonitization to occur over a temperature range of 50–150 °C with 75%–80% and >90% palagonitization occurring at temperatures of 80 °C and 120 °C, respectively. In the Reed Rocks, the greatest palagonitization proportion is ~66% of total primary glass or ~33% of entire sample (Table 1), suggesting that alteration temperatures may well have been <80 °C. Higher temperatures may have been reached at Reed Rock than at South Reed Rock, or there may have been higher water/rock ratios, because there is a greater abundance of palagonitic alteration at Reed Rock (~1%–33%) compared to at South Reed Rock (~2%–7%).

Putative Microbial Bioalteration

Petrographic analysis of thin sections from 13 tuff samples revealed a variety of textures that, compared to other previously published descriptions of marine bioalteration textures and distributions, have conspicuous similarities to the tubular and granular morphological types of microbial alteration (e.g., Fisk et al., 1998a; Furnes and Staudigel, 1999; McLoughlin et al., 2008; Staudigel et al., 2008; Fisk and McLoughlin, 2013). Abundant photographic documentation (Figs. 6–11; Figs. DR1–DR41) is included here to demonstrate that the variety of textures in Reed Rocks tuffs encompasses several of the textures found in seafloor basalts. Referring to the set of biogenicity principles proposed by McLoughlin et al. (2007), the putative microborings described here fulfill at least two of the criteria:

1. Evidence of biogenic morphology and behavior. The Reed Rocks putative bioalteration textures display the following morphologies: wide incursions with mushroom-like termini, and irregular and mossy branching alteration fronts (Fig. DR1 [see footnote 1]); septate divisions, annulations, and spiral or helical filamentous forms (Fig. 6); straight to curvilinear, internal divisions, and bulbous to rough terminal swells and crowns (Fig. 7); rough or disc-shaped terminations (Figs. 8 and 9); ovoid bodies or spherical buds (Figs. 8A and 10); simple, net-work, and palmate branching patterns (Fig. 11); simple, thin, knotted, and tangled patterns (Fig. DR2 [see footnote 1]); irregular granular incursions, alteration fronts of subspherical pits, and bubble textures (Fig. DR3 [see footnote 1]); and directional changes upon encountering another tunnel, fracture, or plagioclase crystal, migration toward olivine grains, and dark opaque contents (Fig. DR4 [see footnote 1]).

GSA Data Repository item 2016075, Figures DR1–DR4, X-ray fluorescence (XRF) geochemistry, point count data, descriptive statistics, and micro- and powder X-ray diffraction (µXRD and pXRD) mineralogy, is available at http://www.geosociety.org/pubs/ft2016.htm or by request to editing@geosociety.org.
Diameters of microtunnels are most commonly 0.5–1.5 µm, but they range from 0.4 to 5 µm (Fig. 12). Tunnel lengths range from 6 to 48 µm. Tunnels from marine environments are typically 1–5 µm in diameter, with lengths of up to 100 µm (Furnes et al., 2001; Fisk and McLoughlin, 2013). The size variation for microtunnels at Reed Rocks is log-normally distributed (Fig. 12). Log-normal size distributions are a common observation in biological systems (e.g., Limpert et al., 2001; van Dover et al., 2003) and have also been observed in tunnel diameter size distributions of oceanic basalts (e.g., Furnes et al., 2007a). Tubular microtunnels are more highly concentrated around vesicles (Figs. 6A–6C, 7A–7D, 7F, 8B, 10A, 10D, and 11A–11C; Figs. DR1B, DR2, and DR4A–DR4B [see footnote 1]), suggesting biological behavior and that these sites may be preferred because structural weaknesses may be exploitable, or because micro-environmental or chemical conditions are more favorable.

SEM imaging revealed irregular tunnel wall surfaces. They unevenly consist of pits, possibly

Figure 3 (continued). (C) Secondary minerals nontronite and chabazite (pXRD). Background subtracted. (D) Distinct secondary pore-filling calcite (µXRD). This also shows a broad elevated portion of the signal from 15° to 40° 2θ produced by the amorphous glass. No background subtraction was performed. See Figure 1 for sample locations.

Figure 4. Abiotic aqueous alteration. (A) Coarse ash pyroclast with a regular banded smooth yellow gel-palagonitic (isotropic) alteration front along the exterior margin (arrow), and an unaltered glass core. From sample FR-12-91A. (B) Abiotic palagonitic alteration front originating from a vesicle surface. From sample FR-12-90. The smooth isopachous fibro-palagonitic (anisotropic) band (arrow) is a later-stage protocrystalline material formed after the amorphous gel-palagonite. The smooth regular alteration fronts of A and B differentiate this aqueous (abiotic) alteration from the irregular granular and tubular textures believed to be formed biologically.
caused by incongruent dissolution, in addition to solid irregular elongate encrustation features (Figs. 9B–9C). These may be the result of a precipitation process whereby insoluble residual and organic chemical components were deposited along the interior of tunnels (Furnes et al., 2007a), or they may be secondary encrustations of smectites.

2. A primary geological context that demonstrates the age and syngenetic of putative biotexture formation. The Reed Rocks microtunnels are only found within fresh volcanic glass pyroclasts. Microtunnels are distributed entirely along surfaces that would have acted as pathways for external water and endoliths such as pyroclast margins, fractures, and vesicles. They are typically perpendicular or near perpendicular with respect to the surfaces from which they originate and also appear to predate infilling of carbonate cement phases, as shown by their radiation from calcite-sealed vesicles (Figs. 6B and 10A).

**Geochemical evidence for biological processing.** EDS analyses indicate that tunnel interiors are slightly depleted in Na, Ca, Mg, Al, and Fe, and either enriched or show no change in K relative to fresh glass (Fig. 8C). Similar depletions of metabolically important elements such as Na, Mg, Fe, and Ca have been documented in association with biotexture textures of in situ ocean basaltic interiors (e.g., Alt and Mata, 2000).

**Distinguishing Biogenic from Abiotic Textures**

**Aqueous alteration (palagonite).** Tubular and granular textures are distinguished from abiotic alteration fronts by their irregular nonsmooth appearance and asymmetric distribution about the fractures or surfaces from which they originate. Aqueous alteration forms planar, regularly banded alteration fronts interacting with fresh unaltered glass symmetrically along fractures and margins (Fig. 4).

**Fractures.** Where tunnels intersect the glass surface, cross sections are generally circular/elliptical. The circular or elliptical walls of a tunnel can be traced into the thin section by moving the focal plane downward. Fractures, however, from which many tunnels originate and are directly juxtaposed, appear as linear two-dimensional expressions of either curved or planar surfaces.

**Ambient inclusion trails.** The morphology of tubular microtunnels in the Reed Rocks can be distinguished from similar tubular textures known as ambient inclusion trails that are produced abiotically. They are differentiated by (1) the absence of metal sulfide or oxide grains at the ends of microtubules, although unlike most oceanic pillow basalts, there is a minor source of oxide crystal inclusions within the basaltic glass; (2) the presence of annulations or ornamentalized and the absence of longitudinal striations that would have been produced by the facets of a mineral grain if it were propelled through the substrate; (3) the absence of angular cross sections; and, (4) at times, the presence of nodal swelling. What is more, the tunnels here commonly have some preferred orientation and indication of biological behavior, unlike ambient inclusion trails, which lack any preferred orientation (Wacey et al., 2008).

There is a single exception to point 1, the absence of grains at the ends of microtunnels, in Reed Rock. In a single tunnel, an oxide grain is found at the terminus (Figs. 13A–13B), but in this case, it is not believed to be a result of ambient inclusion trail formation processes for several reasons. This tunnel originates from the margin of a pyroclast (amorphous, noncrystalline volcanic glass). It has an irregular pitted interior surface, lacks longitudinal striae, and has a variable diameter, most notably shown by...
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Figure 6. (A) Straight, engorged tunnel with septa (arrow) originating from a vesicle. (B) Long, curved tunnels with sparse annulations (arrows). These are rooted on a vesicle that has been sealed with calcite, suggesting tunnel production prior to carbonate precipitation. From sample FR-12-90-1. (C–D) Curvilinear tunnels with spiral filaments or fine ornaments (arrows) along tunnel walls, slightly tapered toward their ends and rooted on vesicles. (E) Smooth, helical tunnels (two right arrows) with bulbous terminal enlargement (left arrow). A, C, and D are from sample FR-12-94B.

Figure 7. Variations of microtunnels with terminal enlargements. (A) Enhanced depth of focus (EDF) image showing close, smooth, thin, straight to curvilinear, constant-width tunnels, with terminal bifurcating crown (upper arrow) and mushroom-like (mid-arrow) enlargements radiating from a vesicle infilled with matrix material. Lower arrow points to smooth, simple, thin tunnel without terminal enlargement. (B) Straight, constant-width tunnel with round terminal bulb (left arrow) and small ovoid body (right arrow) midway along its length. Tunnel emerges from a granular alteration front along a pyroclast margin at right. (C–D) Rough, irregular tunnels with rough, dark terminal crowns, rooted on vesicles. (E) Straight tunnels with round bulbous terminal enlargements (upper arrows) and internal divisions (bottom-left arrow). (F) Thin, directed tunnels curving in a similar direction, with dark terminal crowns (upper two arrows) and slight tapering toward termini. Bottom arrow indicates a kinked tunnel. All are rooted on a vesicle. A and E are from sample FR-12-97E, B–D and F are from sample FR-12-97A.
tapering and then terminal enlargement at its end (Figs. 13A–13B). On the irregular boundaries, small filament structures (Fig. 13C) similar to those found by Banerjee and Muehlenbachs (2003), and irregular pits (Figs. 13B–13D) possibly indicative of biological glass etching (e.g., Thorseth et al., 1995) are present. The tunnel also emerges from what appears to be a granular alteration front at the pyroclast margin (Fig. DR3C [see footnote 1]). The majority of ambient inclusion trails are sealed inside microcrystalline or massive layers and cut off from exterior surfaces of clasts (McLoughlin et al., 2010). There are no examples of terminal enlargements in ambient inclusion trails. Those that do have terminal crystals possess profiles on the distal ends of the trails that are direct images of the crystal-trail interface; hence, the terminus of the trail is a mold of the crystal shape. This is not the case here. Microtunnels have been observed to migrate toward olivine grains (e.g., McLoughlin et al., 2007), and this may be an instance of a tunnel directed toward an oxide grain in search of preferred metabolically important metals such as Fe. Fe is believed to be a key element involved in the biological dissolution of glass (Staudigel and Furnes, 2004).

Additionally, the hydrologic regime of the Reed Rocks tuff also contrasts with that believed to be necessary for ambient inclusion trails to form. Ambient inclusion trails are produced by mineral grains that are driven by high fluid pressures through cryptocrystalline substrates such as cherts producing void tubular trails (Tyler and Barghoorn, 1963; Knoll and Barghoorn, 1974). In order to reach such sustained unidirectional fluid pressures required to initiate pressure solution and drive crystals, it is necessary that the surrounding material be an impermeable closed system. The systems in which ambient inclusion trails have been reported had little or no exposure to fluid circulation (e.g., Tyler and Barghoorn, 1963; Knoll and Barghoorn, 1974; McLoughlin et al., 2010). The tunnels in the Reed Rocks occur within volcanic glass as opposed to chert or phosphorite, and in contrast to the reported occurrences of ambient inclusion trails, these deposits are porous and permeable open systems that were exposed to circulating fluids. This is shown by the profusion of fractures, which connect gas vesicles, the presence of ancillary precipitates, and the concentration of palagonitic and putative bioalteration along fluid-exposed pathways (pyroclast margins, vesicles, and fractures). It is not likely that pressures could build up high enough to initiate solution; therefore, the primary conditions in Reed Rocks lacked the driving force necessary to propel a grain through the glass, producing microtunnels (McLoughlin et al., 2010).

Figure 8. Scanning electron microscope (SEM) and backscattered electron (BSE) images of tubular microtunnels. (A) Enlarged BSE image of box in B showing a smooth tunnel with ovoid cell-sized objects projecting from its margins. These are from the same sample from which the images in Figure 10E were taken. (B) BSE image showing multiple straight and curved, directed tunnels with disc-like terminal enlargements (bottom arrows), radiating from a vesicle at top. Note that several round to irregular-shaped isolated objects are located between tunnels representing normal and oblique cross sections, respectively, through only the terminal enlargements of tunnels intersecting the glass surface. (C) Energy dispersive spectrometry (EDS) element maps of the area depicted in Figure 8B. Change in tone from dark to light indicates an increase in elemental abundance.
**Fluid inclusion trails and radiation damage trails.** It is possible that tunnels can be constructed by exploiting fluid inclusion trails (e.g., Parnell et al., 2005). These may be located within solitary sedimentary quartz or other mineral grains and may be formed by the partial healing of fractures. The Reed Rocks tunnels described here do not occur in any crystalline materials and are only found in basaltic glass. We also find no fluid inclusions, as they are typically not trapped within the glass (McLoughlin et al., 2010). Also, radiation damage trails are potential sites along which tunnels can form. These would be randomly oriented without any directionality, would not display any preference for exterior surfaces, and would likely intersect one another as do fission track trails (McLoughlin et al., 2010). In contrast, the Reed Rocks tunnels display directionality, are strictly associated with external surfaces (margins, fractures, vesicles), and do not intersect one another.

**Bioalteration versus Textural Properties**

To evaluate the relationships between primary and secondary textures and the intensity and type of putative bioalteration, we investigated key textural characteristics, including abiotic aqueous alteration, fresh glass proportions, and porosity (Table 1). With increasing proportions of aqueous (abiotic) glass alteration, we note a general increasing intensity of bioalteration (Fig. 14A). This correlation is generally observed over the full suite of samples ($R^2 = 0.7$).

The most common types of tubular textures at Reed Rocks are simple and branching forms (e.g., Figs. 10A and 11A; Figs. DR2 and DR4 [see footnote 1]). Tunnels with terminal enlargements (Figs. 7–9) are the most abundant type in Reed Rock, but they are virtually absent from South Reed Rock. The terminal enlargement type is also most abundant in samples with the highest proportions of aqueous (abiotic) alteration (Fig. 14B), potentially suggesting that fluid flux and composition are important controlling variables for microtunnel formation (cf. Cousins et al., 2009). If the abundances of alteration phases are a gauge for aqueous alteration intensity and fluid flux, then the greater alteration proportions and precipitate abundances may suggest a greater flux of altering fluids.

The observed correlation between abiotic and putative biotic alteration degree and type suggests palagonitization may lead to an environment favorable to microorganisms and microtunnel formation, or that the processes are linked by similar conditions of alteration. The process of palagonitization involves congruent or incongruent glass dissolution (e.g., Stroncik and Schmincke, 2002; Drief and Schiffman, 2004), which results in the mobilization of elements such as K or Ca (Stroncik and Schmincke, 2002). If these elements are metabolically important to the microorganisms, then circulating fluids may enhance or promote bioalteration. Even if metabolically important elements are relatively immobile, such as insoluble Fe, the fluid composition may change over time, and the type of organisms able to construct tunnels may also potentially change.

**Conditions and Timing of Microtunnel Formation**

The tubular and granular textures at Reed Rock and South Reed Rock appear to have formed both contemporaneous with and subsequent to low-temperature hydrothermal alteration. Some tubular textures propagate beyond abiotic palagonitic alteration fronts and/or contain evidence of alteration within the tunnels (e.g., Fig. DR1 [see footnote 1]), indicating formation temperatures may be bracketed by the inferred lower and upper temperatures of palagonitization (between 25 °C and 80 °C). One sample shows instances of preserved tubular or granular textures found within palagonitized glass (Fig. 15). This suggests that the construction of tubular and granular textures may have taken place soon after emplacement while the volcanic pile was still cooling. Also, a secondary heating event, possibly caused by dike intrusion or the culminating lava lake, may have produced palagonite overprinting of those textures.

Tubular textures radiating from vesicles sealed by calcite, which likely precipitated at temperatures below 80 °C, suggest that they were formed at temperatures above that of calcite precipitation. In open systems, fluid circulation is a sustaining factor for microbial activity, and thus once circulation ceases, so too would microtunnel formation (McLoughlin et al., 2010). This is illustrated in Figures 6B and 10A; construction would have continued until calcite precipitation impeded fluid flow. This suggests that these tunnels were produced when fluids were still freely circulating within the rocks. Because no tunnels are found radiating from vesicles sealed with zeolites (chabazite), they likely formed at least below 80 °C, i.e., the upper limit of zeolite stability.

Granular textures in ocean crust basalts have been documented as dominant in the upper crust at temperatures around 80 °C, whereas tubular textures, generally constituting a smaller portion of total alteration, are most abundant at temperatures near 70 °C (e.g., Furnes et al., 2001, 2007a). The inferred temperature range of the Reed Rocks fits well within the range in which microbial life is known to exist (Stetter et al., 1990), although the conditions here may exclude hyperthermophiles that live above 80 °C (Brock, 1978; Stetter et al., 1990; Stetter, 2007).
The presence of tunnels propagating from fractures, vesicles, and margins not associated with abiotic palagonitic alteration, and with no evidence of alteration within them, suggests microtunnel formation continued at temperatures below 25 °C, the lower temperature of palagonite formation. Microtunnel formation also appears to be stimulated in basaltic glass in marine environments (Thorseth et al., 1995, 2001, 2003; Furnes et al., 1996, 2001, 2005, 2007a, 2007b; Furnes and Staudigel, 1999; Fisk et al., 1998a, 2003; Banerjee and Muehlenbachs, 2003, 2011; Torsvik et al., 1998; Walton, 2008). Microtunnel formation also appears to be stimulated in basaltic glass (Cousins et al., 2009). Such observed differences may be the result of contrasting biomass, nutrient, or temperature conditions of the alteration fluids or aqueous alteration intensity.

Microtunnel Formation in Marine versus Nonmarine Environments

Tubular and granular textures readily form in basaltic glass in marine environments (Thorseth et al., 1995, 2001, 2003; Furnes et al., 1996, 2001, 2005, 2007a, 2007b; Furnes and Staudigel, 1999; Fisk et al., 1998a, 2003; Banerjee and Muehlenbachs, 2003, 2011; Torsvik et al., 1998; Walton, 2008). Microtunnel formation also appears to be stimulated in basaltic glass (this study) and impact glasses (Sapers et al., 2014) in lake environments. Glacial freshwater, however, may be the least conducive to microtunnel formation (Cousins et al., 2009). If nutrient acquisition is a major pressure that makes boring advantageous (Kiene et al., 1995), it might be expected that nutrient-poor glacial meltwater environments would force microbes to obtain essential nutrients such as Fe from basaltic glass. A possible explanation may relate to the biomass of the water.
A greater biomass in marine and lake water would mean more microbes are introduced into the environment, and therefore there may be more competition for nutrient resources and more predation. Boring into a rock could provide a means of protection from other predatory macro- and microorganisms (e.g., fungi; Priess et al., 2000) and a means of obtaining essential nutrients.

Observed microtunnel differences between glacial and marine or lake environments may also be related to temperature. In oceanic basalts, optimum growth conditions for relevant microbes appear to be ~60–70 °C, indicated by a maximum of tubular alteration at crustal depths in this temperature range (Furnes et al., 2001, 2007a). Here, we find that microtunnel formation occurred mainly at 25–80 °C. Subglacial meltwater would be ~0 °C; therefore, temperature may also be a major factor in microtunnel formation. Our findings also indicate that the intensity of putative bioturbation is related to the intensity of aqueous (abiotic) alteration (Fig. 14), a factor also considered by Cousins et al. (2009) and Cockell et al. (2009b). Aqueous alteration (palagonitization) is enhanced at higher temperatures (Jakobbson and Moore, 1986; Crovisier et al., 1987), and the correlation between putative biotic and abiotic alteration suggests that a relatively narrow temperature range promotes microtunnel formation. Other factors linked to rate and degree of abiotic alteration include fluid flux rate, water/rock ratio, microchemical and pH changes in alteration fluids, and mineralization (Jakobsson and Moore, 1986; Crovisier et al., 1987, 1992; Thorseth et al., 1991, 1992, 1995; Staudigel et al., 1991) and these may also influence microtunnel formation. In environments subject to high rates of mineralization, for example, microboring may be a means to avoid mineralization that would entomb microbes (Cockell and Herrera, 2008). This might explain the presence of microtunnels radiating from calcite-sealed vesicles, where the prospective boring organisms may have been avoiding calcite mineralization. Microborings have been extensively observed in substrates related to locations with high mineralization rates (Schneider and Le Campion Alsumard, 1999), and hydrothermal environments give evidence of a selection pressure for demineralization in organisms such as iron oxidizers that are usually found in such environments (Cockell and Herrera, 2008).

Given that the geochemical and microbiological systems in marine and lacustrine settings are different, it might be expected that the morphologies of putative microborings would also differ. Here, we demonstrate that this is not
the case. Cousins et al. (2009) similarly observed no difference between the types of putative microbial textures found in either fresh glacial meltwater or marine altered basalts. Microbes found in marine, lacustrine, and glacial melt settings may thus dissolve or etch basaltic glasses using a common mechanism that is independent of the alteration fluid.

Relevance to Mars

The pluvial Fort Rock Lake setting is relevant to understanding analogous Martian environments, including the Sheepbed mudstone member of the Yellowknife Bay Formation, which was examined by the Mars Science Laboratory (MSL) Curiosity rover in Gale Crater (Grotzinger et al., 2014). The Sheepbed mudstone includes basaltic material and is interpreted to be an ancient shallow lacustrine deposit (Grotzinger et al., 2014) and may include an ash-fall component (McLennan et al., 2014). Phyllosilicate minerals identified by the CheMin instrument (XRD) in the Sheepbed mudstone suggest relatively neutral pH waters that could have persisted throughout its aqueous history. The Sheepbed mudstone also lacks collapsed and highly ordered illite or chlorite unrelated to partially intercalated clay or incipient chloritization in the Cumber land sample (Vaniman et al., 2014). On Earth, such minerals typically require alteration temperatures greater than ~60–80 °C (e.g., Chang et al., 1986), suggesting moderate alteration temperatures below ~60–80 °C (Vaniman et al., 2014). This is within the temperature range that we infer for the formation of tubular and granular textures at Reed Rocks. The Sheepbed lake environment likely underwent episodic drying (Grotzinger et al., 2014), like the waxing and evaporative waning of terrestrial pluvial lakes in the western United States, which were probably related to Pleistocene glacial fluctuations (Martin et al., 2005).

Another analogous Martian site to the Reed Rocks site is the Home Plate outcrop that was examined by the Spirit Mars Exploration Rover (MER) in Gusev Crater, where geological, textural, and geochemical observations suggested that the deposits are variably reworked hydrovolcanic basaltic tephra (Squyres et al., 2007; Schmidt et al., 2008). Differences in mineralogical and geochemical composition (i.e., olivine content, and Cl concentration) across the ~80 m Home Plate outcrop are consistent with it having experienced both high- and low-temperature aqueous alteration (Schmidt et al., 2009). Nearby silica-rich deposits were also interpreted to have formed under hydrothermal conditions through acidic bleaching or sinter deposition, indicating ancient aqueous environments (Squyres et al., 2008).

Also relevant is the widespread finding of an amorphous component in deposits across the Martian surface and in Martian dust (Morris et al., 2006; Squyres et al., 2007; Yen et al., 2008; Schmidt et al., 2009; Bish et al., 2013; Grotzinger et al., 2014; McLennan et al., 2014; Vaniman et al., 2014). The amorphous component may include volcanic glass or devitrified altered products of volcanic glass, and it consists of nanophase Fe-oxides and an amorphous palagonite that is commonly observed in terrestrial altered basaltic glassy deposits (Morris et al., 2001, 2006). Other common products of the alteration of basaltic glass on Earth, including saponitic smectite and zeolite minerals (Ehlmann et al., 2009), have also been identified on the Martian surface.
Candidate microborings in Oregon basaltic tuffs

The positive correlations between abiotic aqueous alteration and the intensity of potential bioalteration and abundance of microtunnels with terminal enlargements point to a direct influence of fluid flow and composition. The intensity of the aqueous alteration experienced by the basaltic glass and the flux of altering fluids appear to promote microtunnel construction. The association of certain microtunnel morphologies with more highly altered samples suggests that the altering fluid chemical composition was likely modified more substantially than those that experienced less aqueous alteration, and that this probably had an influence on the processes by which microtunnels were produced or possibly the type of constructing organisms.

**CONCLUSIONS**

(1) The Reed Rocks hydrovolcanic tuffs in the Fort Rock volcanic field contain various tubular and granular textures that are similar in size, morphology, and distribution to previously described bioalteration in marine and subglacial marine transition zones and are characteristic of endolithic microboring biogenicity. We argue that this is the first account of putative endolithic microborings in a nonmarine, non-subglacial continental setting, and this study contributes to expanding the range of environments where tubular and granular textures have been documented.

(2) Based on textural relationships between secondary phases and putative microbial textures, the Reed Rocks tubular microtunnels and granular textures are inferred to have formed predominantly in neutral to alkaline, saline fluids at temperatures between 25 °C and 80 °C. Hydrothermal/aqueous alteration occurred in a low-temperature thermal regime (≤80 °C).

(3) We note that in addition to the significant presence of microtunnels in the Reed and South Reed Rock tuffs, examinations of several other tuff deposits throughout the Fort Rock volcanic field have revealed similar textures. Microtunnel formation is not just a locally isolated phenomenon in the Reed Rocks, and it is in fact a significant component of the regional geologic history. If these features are widespread in the Fort Rock volcanic field, then further investigation is required to compare local geology, textural and mineralogical characteristics, and putative bioalteration of other locations to those found in Reed Rocks and oceanic and subglacial basalts. Assessing the relationships between these qualities and the intensity and type of tubular and granular textures will help in understanding the controls on their formation and potentially habitable conditions.

(4) The Fort Rock lake has geologic, environmental, geochemical, and mineralogical parallels with locations on Mars, including rover landing sites in Gale and Gusev Craters. Such analogous characteristics consist of confined lacustrine settings and other aqueous environments with circumboreal pH conditions; volcanically derived basaltic substrates with amorphous phases probably consisting in part of glass; and evidence of low-temperature hydrothermal alteration as well as similar alteration products such as saponitic smectites and hydrothermal alteration as well as similar alteration products such as saponitic smectites.

**ACKNOWLEDGMENTS**

Funding for this research was provided by the Canadian Space Agency (CSA) Astromaterials Training and Research Opportunity (ASTRO), an Ontario Graduate Scholarship (OGS), and Natural Sciences and Engineering Research Council (NSERC) Canadian Graduate Scholarship-Master’s (CGS-M) to Nikitczuk, as well as NSERC Discovery grant to Schmitt. We thank Nevena Novakovic for assisting in the collection of samples and field observations in Fort Rock, Oregon. Thanks go to Marty Oulette of the Brock University petrographic laboratory for thin section preparation. The support of Alex Rupert during micro–X-ray diffraction analyses at the University of Western Ontario is greatly appreciated. For access to and assistance at the Zircon and Accessory Phase Laboratory (ZAPLab) at the University of Western Ontario during scanning electron microscope and energy dispersive spectrometry analysis, we are grateful to Desmond Moser and Ivan Barker. Thanks also go to Marc Beauchamp for helping with enhanced depth of focus imaging at the University of Western Ontario. Also, we thank Martin Fisk for taking the time to review the early stages of the manuscript and provide valuable feedback.

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Nikitczuk et al.


Candidate microborings in Oregon basaltic tuffs


Science editor: Christian Koberl
Associate editor: Henning Depvik

Manuscript received 9 July 2015
Revised Manuscript received 20 January 2016
Manuscript accepted 26 February 2016

Printed in the USA