

Impact-induced impoverishment and transformation of a sandstone habitat for lithophytic microorganisms

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(Received 13 October 2006; revision accepted 08 May 2007)

Abstract—Sandstones are a common habitat for lithophytic microorganisms, including cryptoendoliths. We describe laboratory experiments on the colonization of impact metamorphosed sandstones from the Haughton impact structure, Canadian High Arctic. Colonization experiments with the coccoid cyanobacterium, *Chroococcidiopsis* sp. and the motile gram-positive bacterium *Bacillus subtilis*, show that, in contrast to initially low porosity crystalline target rocks, which can become more porous as a result of impact bulking, by closing pore spaces the sedimentary cryptoendolithic habitat can be impoverished by impact. However, the heterogeneous distribution of collapsed pores, melt phases, and subsequent recrystallization, results in heterogeneous colonization patterns. Cavities and vesicles formed during melting can yield new habitats for both cryptoendoliths and chasmoendoliths, manifested in the natural cryptoendolithic colonization of shocked sandstones. By contrast, post-impact thermal annealing and recrystallization of impact melt phases destroys the cavities and vesicles. In extreme cases, complete recrystallization of the rock fabric makes the material suitable only for epilithic, and potentially hypolithic, colonists. These experiments further our understanding of the influence of the target lithology on the effects of asteroid and comet impacts on habitats for lithophytic microorganisms.

INTRODUCTION

The porosity and permeability of rocks have a crucial influence on their suitability as habitats for microorganisms. When pore spaces within a rock interior are linked (i.e., when the rock is permeable) they can become hosts to “cryptoendoliths” that invade the rock and grow within the rock structure (Fig. 1, Golubic et al. 1981). If the rock allows sufficient penetration of photosynthetically active radiation (PAR), distinct bands of photosynthetic colonists can become established (Friedmann 1980).

Colonization of the interior of rocks is also made possible by macroscopic fractures or openings from the surface (Broady 1981a; De los Rios et al. 2005), which can be formed by a diversity of processes including aeolian and fluvial weathering and freeze-thaw. The organisms that inhabit these openings are “chasmoendoliths” (Fig. 1).

The colonization of the surface of a rock by “epiliths” is common and requires no specific geological characteristics, other than that the rock is not toxic. Similarly, rocks can be colonized on their underside by “hypoliths” (e.g., Berner and

Evenari 1978; Broady 1981b; Smith et al. 2000; Schlesinger et al. 2003) (Fig. 1); in the case of photosynthetic organisms, this requires that the rock is translucent or that spaces are created around the edges of the rock for light to penetrate to its underside by, for example, freeze-thaw cycles (Cockell and Stokes 2004; 2006).

It is evident that asteroid and comet impacts can have an important influence on micro-habitats for rock-dwelling microorganisms (Cockell et al. 2002; 2005). Impact bulking commonly increases the fracture space within rocks, which provide a greater abundance of habitats for chasmoendoliths (Cockell et al. 2005). In some instances, the increase in permeable space within the target material can increase the habitat available for cryptoendoliths. It has previously been reported how this type of alteration, in combination with an increase in rock translucence, has formed cryptoendolithic habitats for photosynthetic colonists in Precambrian gneiss in the Haughton impact structure, which is not otherwise a suitable habitat for them (Cockell et al. 2002). This finding constituted the first empirical evidence for the formation of a microbial habitat specifically by asteroid or comet impact.

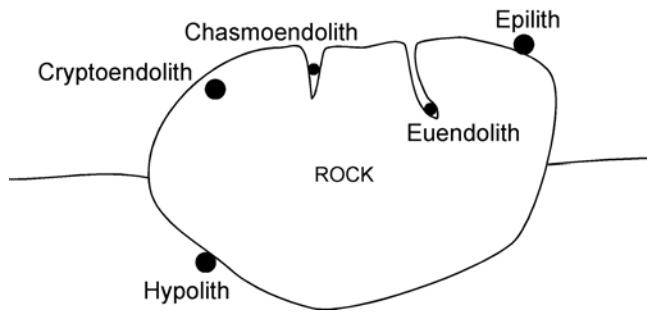


Fig. 1. Lithophytic habitats (adapted from Golubic et al. 1981). Cryptoendoliths inhabit the interstices of the rock; chasmoendoliths inhabit macroscopic cracks; epiliths inhabit the surface; hypoliths inhabit the underside; euendoliths are organisms that actively bore into rocks.

It is clear that the fate of highly porous substrates versus low porosity substrates during impact is different (Kieffer 1971). In the former case, more of the impact energy must be taken up in pore collapse. Thus, an examination of the effects of asteroid and comet impacts on the colonization of porous sedimentary target lithologies can provide a model that will help understand more generally the effects of impacts on the colonization potential of rocks.

Of minerals that offer habitats for cryptoendoliths, sandstones are particularly widespread. Endolithic communities within sandstones have now been described from many surface locations around the world, including hot and cold deserts, and even buildings (e.g., Blackhurst et al. 2005; Büdel et al. 1994, 2004; Friedmann 1980, 1982; Grondona et al. 1997; Kurtz and Netoff 2001; Omelon et al. 2006; Palmer et al. 1991; Uwins et al. 1998; Weber et al. 1996; Wessels and Büdel 1995). Microorganisms are known to inhabit subsurface sandstones, where the porosity and flow of nutrient and redox couple-containing ground waters can supply them with their metabolic requirements (e.g., Fredrickson et al. 1997; Colwell et al. 1997; Tseng and Onstott 1997; Onstott et al. 1998).

Thus, understanding how impact metamorphism alters the characteristics of sandstones and their subsequent suitability for microbial colonization is of great interest for understanding the nature of surface and deep subsurface rocky habitats for microorganisms, past and present. Furthermore, the discovery of basaltic sandstones on Mars (e.g., Squyres et al. 2004) shows that such investigations yield insights into habitability elsewhere.

In this paper, laboratory experiments are described in which we investigated the effects of impact metamorphism on the microbiological colonization of sandstones from the Haughton impact structure, Canadian High Arctic.

MATERIALS AND METHODS

Characteristics of the Field Site

The Haughton impact structure is located on Devon

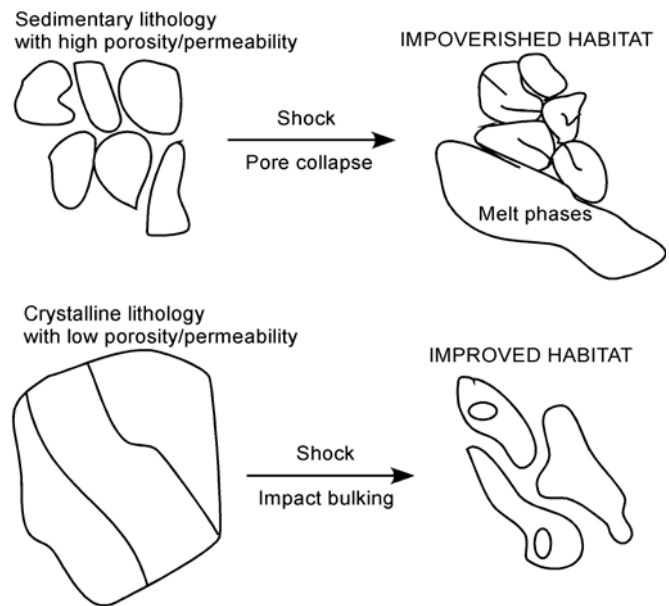


Fig. 2. Summary of the hypothesis tested in this work.

Island, Nunavut, in the Canadian High Arctic ($75^{\circ}22'N$ and $89^{\circ}41'W$). Based on geophysical data, the structure has an apparent diameter of about 24 km (Pohl et al. 1988), although recent detailed structural mapping indicates that a value of 23 km is more accurate (Osinski and Spray 2005). The structure was formed in a target sequence dominated by a thick series (~1880 m) of Lower Paleozoic marine sedimentary rocks of primarily carbonates, dolomite and limestone, overlying crystalline basement Precambrian granites and gneisses (Thorsteinsson and Mayr 1987; Osinski et al. 2005a). The crater interior is filled with allochthonous impact-melt breccias, which comprise a groundmass of carbonate and silicate melt phases enclosing clasts from various parts of the pre-impact target sequence to depths of ~2 km (Grieve 1988; Osinski and Spray 2001; Osinski et al. 2005b). This unit has a maximum preserved thickness of ~125 m and covers an area ~60 km² (Scott and Hajnal 1988). The original dimensions of the impact-melt breccia deposit are estimated to be greater than 200 m in thickness and ~12 km in diameter (Osinski et al. 2005b). In the eastern part of the crater, the impact-melt breccia deposits are divided into a series of discrete outcrops separated from the main deposits in the central part of the crater by a system of broad (up to ~1 km wide) alluvial terraces associated with meanders of the Haughton River.

The sandstones described in this paper were collected from the impact-melt breccia hills in the central region of the crater, as described in Osinski (2007).

Samples Used for Laboratory Experiments

Samples corresponding to different shock classes collected during the 1999 to 2004 field seasons were used for colonization experiments. These samples represent individual

Table 1. Observations and comments on the colonization of different shock classes of sandstones from the Haughton impact crater. For a description of porosity measurements see Osinski (2007).

Class	Pressure range (GPa)	Porosity (%)	Observations on lithophytic colonization in the laboratory	General comments on lithophytic colonization
1a	<3	7–23	Cryptoendolithic colonization unimpeded in rock.	Rock is indistinguishable from unshocked material. Colonization determined by porosity and cementing of grains.
1b	3–5.5	2–5	No interior colonization observed. Colonization restricted to epilithic growth (Fig 3c).	Collapse of pore space occurs. Reduction in porosity will impede cryptoendolithic colonization in some regions. Fracturing of grains can maintain some permeability.
2	5.5–10	4–7	Heterogeneous cryptoendolithic colonization observed. Regions with some permeability allow for cryptoendolithic colonization. Other regions completely impede colonization (Figs. 3d, 3e).	Heterogeneities in grain compression and the presence of impact-generated micro-breccias form areas where cryptoendolithic colonization is possible. Other regions where grain compression and porosity is reduced will limit colonization to chasmoendolithic/epilithic colonization.
3	>10 –<20–25	6–21	Colonization in many regions restricted to chasmoendolithic colonization of vesicular regions. Where vesicles are linked cryptoendolithic colonization is observed with <i>Bacillus</i> sp.	Natural cryptoendolithic colonization by <i>Gloeocapsa</i> sp. is observed in samples from the field (Figs. 3g and 4d).
4	>20	18–30	Colonization in many regions restricted to chasmoendolithic colonization of vesicular regions (Fig. 3f). Where vesicles are linked cryptoendolithic colonization is observed with <i>Bacillus</i> sp.	As with class 3, cryptoendolithic colonization is possible where vesicles are linked, representing also a form of “cryptic” chasmoendolithic colonization. Some recrystallized regions may completely impede colonization.
5a	20–30	30–36	Colonization in many regions restricted to chasmoendolithic colonization of vesicular regions. In many cases, vesicularization may be more pronounced than lower shock levels leading to increased colonization potential (Fig. 5).	Habitat predominantly glass. Colonization restricted to chasmoendolithic colonization of vesicular regions. Depending on linked vesicles cryptoendolithic colonization by some organisms may be possible.
5b	>30–35	44–58	Colonization in many regions restricted to chasmoendolithic colonization of vesicular regions.	Habitat predominantly glass. Colonization restricted to chasmoendolithic colonization of vesicular regions. Depending on linked vesicles cryptoendolithic colonization by some organisms may be possible.
6	>30–35	4–9	No interior colonization observed. Colonization restricted to epilithic growth (Fig 3h).	Complete recrystallization and loss of vesicles—both cryptoendolithic and chasmoendolithic colonization will be impeded. Epilithic and hypolitic colonization possible.

clasts from the impact-melt breccias. Shock pressures and class of samples were determined according to the work presented in Osinski (2007) (Table 1). Samples were used that matched classes 1 to 6. Samples of sandstone were cut into blocks of approximately $2 \times 2 \times 2$ cm and three samples of each class were used in each experiment. Beacon sandstones from the Dry Valleys of the Antarctic were used as control substrates. These sandstones naturally host cryptoendolithic communities which display well-developed stratification (Friedmann 1980; Johnston and Vestal 1989). In many of the rocks, a black layer of lichen colonization (Fig. 3a) is observed. Many of them also host algal, cyanobacterial, and fungal colonists. The Beacon Supergroup sandstone is a Gondwanaland sediment formed during the Devonian and Jurassic (400–180 million years ago) and it is widely distributed near the tops of mountains in the Ross Desert in the McMurdo Dry Valleys region of Southern Victoria Land, Antarctica (Barrett 1991). The sandstones have a conspicuous iron stain.

Organisms and Experiments on the Colonization of Rocks

To assess the effects of shock metamorphism on the potential for colonization the cyanobacterium *Chroococcidiopsis* sp. CCME 029 was used as model organism. The desiccation resistant, ionizing radiation-resistant phototroph, *Chroococcidiopsis* (order *Pleurocapsales*, Rippka et al. 1979, order *Chroococcales*, Komárek and Anagnostidis 1998), is thought to be one of the most extreme-tolerant cyanobacteria (Billi and Grilli-Caiola 1996a, b). The unicellular, non-motile cyanobacterium is found in hot deserts such as the Negev in Israel and cold deserts such as the Ross Desert of the Antarctic (Friedmann and Ocampo-Friedmann 1985; Büdel and Wessels 1991).

In its natural environment the organism often colonizes microscopic fissures (chasmoendoliths) and structural cavities (cryptoendoliths) of rocks or it forms biofilms under pebbles in desert regions. Thus, it is an ideal model organism with which to evaluate lithophytic colonization.

Chroococcidiopsis strain CCME 029 was obtained

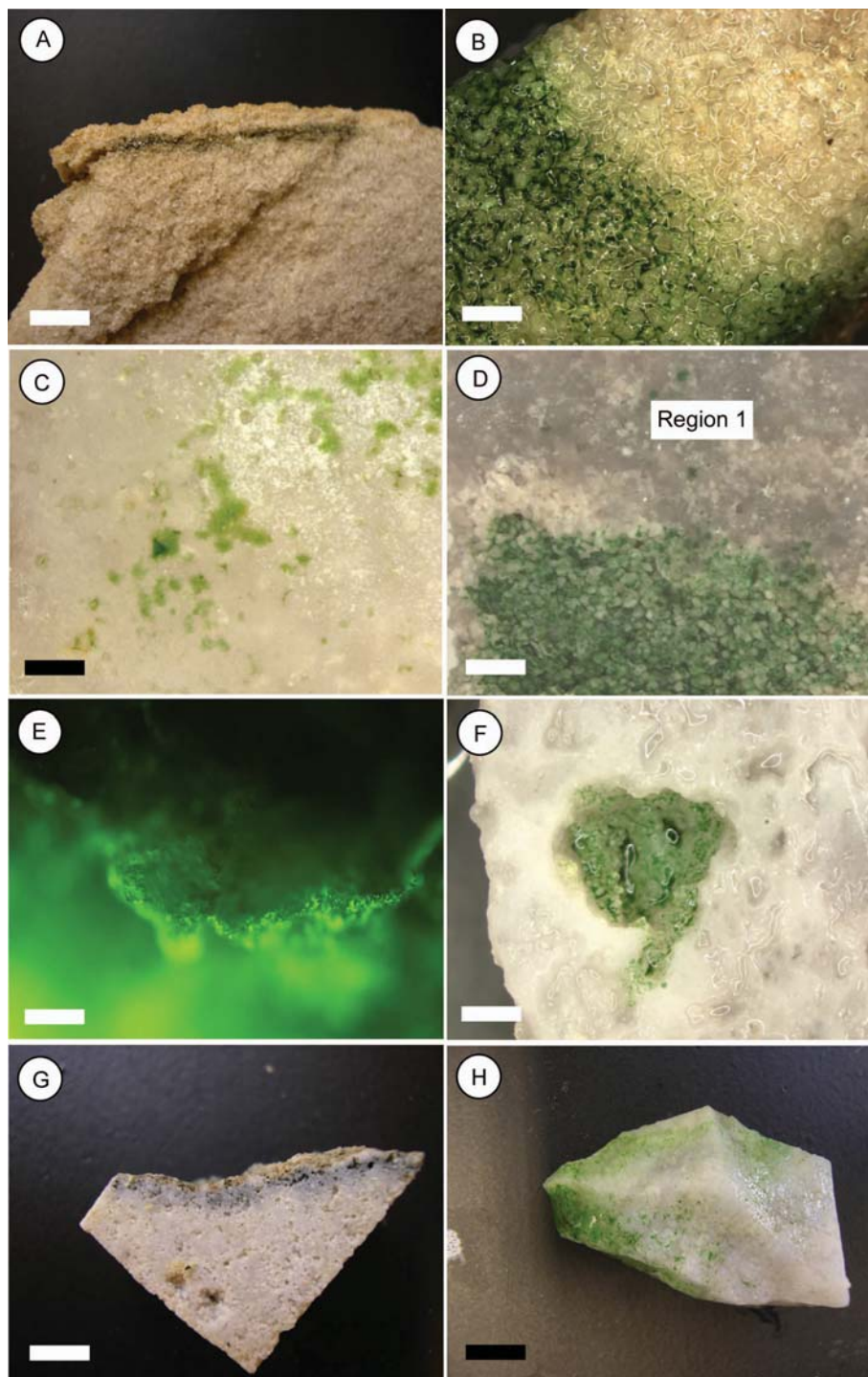


Fig. 3. Effects of impact shock on colonization of sandstones. a) Natural cryptoendolithic colonization of Beacon sandstones from the Dry Valleys of Antarctica (see, e.g., Friedmann 1980 for a description). Black layer is a lichen layer within rock interstices. Scale bar 1 cm; b) Colonization front moving through the interstices of Beacon sandstone (Antarctica) inoculated with *Chroococcidiopsis* sp. 029. Scale bar 0.2 cm; c) Epilithic colonization of class 1b rock. No crypto- or chasmoendolithic colonization of the material is possible. Scale bar 0.5 cm; d) Impeded colonization front of *Chroococcidiopsis* in sandstone (class 2) blocked by "Region 1." Scale bar 0.2 cm; e) Impeded colonization front of *Bacillus subtilis* (seen here as green, stained with Syto 9) in sandstone (similar location to [d]). Scale bar 0.2 cm; f) Chasmoendolithic colonization of vesicles by *Chroococcidiopsis* in sandstone (class 4). Scale bar 0.5 cm; g) Natural cryptoendolithic colonization of class 3 shocked sandstone from Haughton by *Gloeocapsa* sp. Scale bar 1 cm; h) Epilithic colonization of class 6 rock. No crypto- or chasmoendolithic colonization of the material is possible. Scale bar 0.5 cm.

from the Culture Collection of Microorganisms from Extreme Environments (CCMEE) at the University of Rome "Tor Vergata." Stock cultures of the organism were grown in BG-11 medium (Rippka et al. 1979) under an 18:6 h light/dark (LD) cycle with a light intensity of 50 $\mu\text{mol}/\text{m}^2/\text{s}$ and a temperature of 29 °C for one month. The typical diameter of cells grown in nutrient replete medium is $\sim 3 \mu\text{m}$, although the cells often form tetrads and multi-celled colonial forms.

Three sandstone blocks from each shock class were inoculated with 0.5 mL of cultured cells (with an estimated 1×10^6 cells/mL) and placed into a Petri dish containing BG-11. The BG-11 filled the dish so that half of the rock sample was submerged. The inoculated rocks were incubated in the conditions described above. After 60 days the colonization patterns in the rocks were observed by optical dissecting microscope (magnification, 10–40 \times).

In addition, some samples were colonized with *Bacillus subtilis* subsp. *subtilis*, a gram-positive spore-forming microorganism commonly found in soils. The bacterium was obtained from the DSMZ (Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany) (DSM no. 10). It was grown either on tryptic soy agar (TSA) plates or in broth culture. In either case, the organisms were grown at 29 °C. This organism was selected because its size ($\sim 1 \mu\text{m}$ long) can be considered a proxy for many non-photosynthetic prokaryotes inhabiting rocks. Its motility enables it to swim through the intergrain space and fractures within rocks, allowing us to assess the interconnectedness (permeability) of spaces within impact-altered rocks and thus their suitability for colonization.

Similarly to the experiments with *Chroococcidiopsis* sp., rock samples were inoculated with *Bacillus* sp. in Petri dishes containing TSA broth. On account of the faster doubling time of *Bacillus* sp. compared to *Chroococcidiopsis* sp., the rocks were inoculated for 48 h before being observed.

To visualize the *Bacillus* cells the rocks were stained by soaking them in Syto 9 DNA binding dye according to the manufacturers instructions (Invitrogen, Paisley, UK) and observed them on the rock using a Leica DMRP microscope equipped with epifluorescence (Leica Microsystems, Bensheim, Germany). Stained cells were observed fluorescing green using an excitation waveband of 450–490 nm (Leica filter cube I3) and an emission long band cutoff filter of $>515 \text{ nm}$.

Both cyanobacterial biofilms occurring naturally in shocked sandstones and the laboratory colonized rocks were examined by scanning electron microscope (SEM). The SEM was a Quanta 3-D dual beam FIBSEM (FEI, Oregon, USA). Samples of the naturally colonized rocks were cut into small blocks with a rock saw ($\sim 1 \text{ cm}^3$), by cutting the rock perpendicular to the colonized region. The rocks were attached to aluminum sample stubs. Samples were carbon coated (15–20 nm thickness) and the colonized region of the rock was examined in both secondary and backscattered

mode. The geological context of natural biofilms was examined using energy dispersive spectroscopy (EDS) and analysis with the software, Inca (Oxford Scientific Instruments, Oxford, UK).

RESULTS

At shock levels of less than 3 GPa (class 1a), cryptoendolithic colonization was unimpeded. Intergrain porosity is retained, allowing for cryptoendolithic colonization in a similar manner to control material (Figs. 3a and 3b). At shock levels between 3 GPa and ~ 5.5 GPa, loss of porosity reduces the suitability for colonization. We did not observe cryptoendolithic or chasmo-endolithic colonization of class 1b samples in the laboratory. Only epilithic colonization was possible in the samples we examined (Fig. 3c).

At shock pressures between ~ 5.5 and 10 GPa (class 2) porosity is lost, consistent with Hugoniot data (Kieffer 1971). Pore collapse causes the intergrain space to be reduced to below the size of typical photosynthetic and non-photosynthetic colonists ($\sim 1\text{--}3 \mu\text{m}$). However, the shock effects are heterogeneous, and we found that this led to heterogeneous colonization patterns. Some regions of the rock remained sufficiently porous to allow colonization. Whereas in unaltered sandstones the colonization front proceeds unimpeded, such as that we observed in Beacon sandstones from the Antarctic (Fig. 3b), in sandstones shocked to class 2, the colonization front, where it can become established (e.g., in brecciated areas), is often impeded by collapsed pore spaces, such that neither *Bacillus* or *Chroococcidiopsis* spp. were able to invade the region of the rock in which porosity is lost (Figs. 3d, 3e; Region 1). Scanning electron microscopy reveals the region of pore collapse to be devoid of access points for microorganisms (Fig. 4a).

At shock pressures greater than 10 GPa the rocks are rendered vesicular. In the laboratory, in class 3 and 4 rocks, *Chroococcidiopsis* growth was often confined to vesicular regions, resulting in distinctive chasmoendolithic colonies (Figs. 3f, 4b). However, *Bacillus* was able to move from one macroscopic vesicle to another (data not shown), resulting in colonization throughout the rock. Class 3 and 4 rocks were characterized by regions of recrystallized glass in which colonization was not observed between the vesicles.

In the natural environment class 3 shocked sandstones can host cryptoendoliths. Colonization was observed to a depth of $3 \pm 1 \text{ mm}$ in one vesiculated sample (Fig. 3g). The colonists were dominated by the cyanobacterium *Gloeocapsa* sp., as determined by optical microscopy, which form a coherent biofilm in the interior of the rock (Figs. 4c–e). This type of colonization should be distinguished from colonization in unshocked sandstones (Figs. 3a, 3b), which occurs along the intergrain space.

At sufficiently high shock pressures (>30 GPa, class 6), the laboratory experiments show that the material is

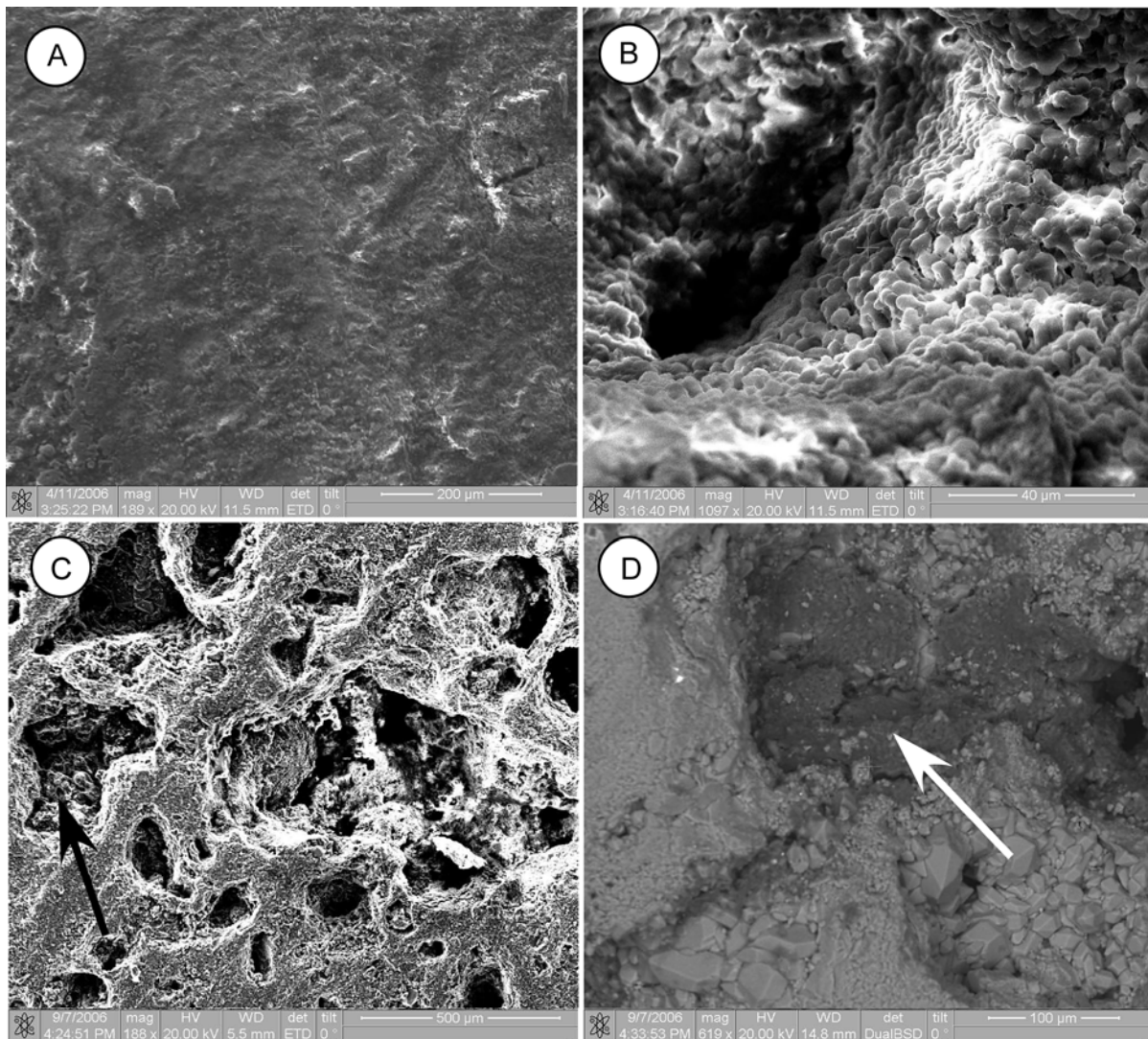


Fig. 4. Scanning electron microscope images. a) Secondary electron image of surface of “Region 1” in Fig. 3d; b) Secondary electron image of chasmoendolithic colonization of vesicle by *Chroococcidiopsis* biofilm (as shown in Fig. 3f); c) Secondary electron image of vesicles in class 3 shocked sandstone (Fig. 3g) which are naturally inhabited by cyanobacterial biofilms (arrow); d) Backscattered electron image of *Gloeocapsa* sp. biofilm (Fig. 3g) within a field of recrystallized quartz crystals (arrow).

recrystallized and rendered sufficiently homogenous to completely impede interior colonization (Fig. 3h). Colonization of class 6 rocks was restricted to epilithic colonization.

DISCUSSION

Sandstone lithologies are common habitats for cryptoendolithic microorganisms. During an asteroid or comet impact into a sandstone target a proportion of the impact energy is taken up by pore collapse (Kieffer 1971; Kieffer et al. 1976). Thus, we would hypothesize that impact events would transform a potentially suitable cryptoendolithic habitat into one that is unsuitable (Cockell et al. 2005). To test this hypothesis we examined the colonization of sandstone rocks that had experienced

differing shock pressures in the Haughton impact crater, Canadian High Arctic. We summarize our findings in Fig. 5 and Table 1.

In low shocked sandstones, where shock levels are less than 10 GPa, pore collapse generally impeded colonization, as we expected. Pore collapse is thought to occur by rearrangement of grains and their plastic deformation into pore spaces (Kieffer et al. 1976). In any region of shocked sandstone where low or zero porosity impedes microbial colonization, growth could be restricted to epilithic growth, or, where sufficient light can penetrate to the underside either through the rock or around its edges, hypolithic colonization.

However, in practice, at pressures between 5.5 and 10 GPa, the results show that the shock lithification of the sandstones is not homogenous. Some regions of the rock possess relatively high porosity and open pore spaces with

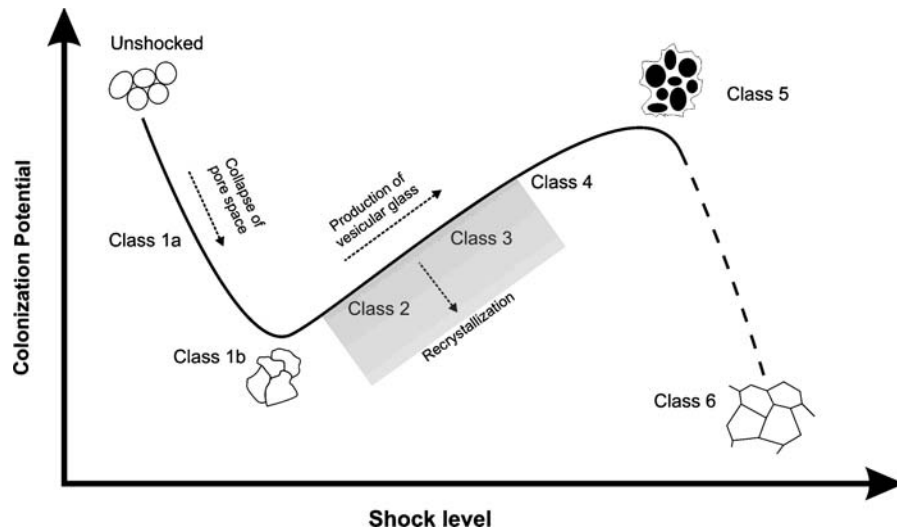


Fig. 5. Schematic diagram illustrating the potential for colonization of sandstones with respect to shock level. The colonization potential observed in the laboratory is consistent with the porosity data (see Table 1).

throat sizes greater than the size of microorganisms ($>1 \mu\text{m}$). Optical microscopy reveals that this is due to a combination of factors, including the generation of porous in situ microbreccias during deformation of the sandstone, and the partial retention of original porosity in isolated enclaves. In other regions, pore collapse leads to a jigsaw-like arrangement of grains, where inter-grain space is lost (Kieffer 1971; Osinski 2007). Some regions in this shock range begin to display localized formation of silica glass, which fills pore spaces and further reduces both porosity and permeability.

We expected that at shock pressures greater than 10 GPa, colonization of the interior of rocks would be completely prevented by pore collapse and glass formation. However, instead, the heterogeneous shock effects result in material that is heavily vesiculated. The vesicles, which Kieffer (1971) attributed to exsolution of water, render regions of the material suitable for endoliths. The proportion of vesiculated glass increases with increasing shock pressure up to ~30 GPa (class 5 rocks).

In many of the vesiculated samples, the movement of *Bacillus subtilis* throughout the rock suggested that the vesicles were interconnected. This explains the observation of the natural colonization of class 3 shocked rocks by *Gloeocapsa* spp. The confinement of the *Chroococcidiopsis* to one region in the laboratory experiment in the class 4 sample we examined might be because the cells did not have time to penetrate throughout the rock, or the inoculated vesicles were not linked to others in this specific case. The thick polysaccharide-rich biofilms produced by *Chroococcidiopsis* and the low doubling time (~4 days) likely impede their movement throughout the restricted spaces that link vesicles within the rock in the time frame of the experiments conducted here.

Optical and SEM microscopy of the class 3 and 4 rocks studied here revealed a further complication. Many of these

rocks contain irregular and isolated regions where the melt phases are partially or completely recrystallized. This can be ascribed to post-impact thermal annealing of the clasts in the hot impact-melt breccias. These recrystallized regions contain no porosity, thus inhibiting colonization. The degree of thermal annealing will therefore influence the subsequent permeability of the rock to colonists.

Similarly to class 1b rocks, growth in class 6 rocks was restricted to epilithic colonization. It is unclear whether class 6 rocks signify higher shock pressures or if this is a post-impact thermal feature.

The results show that the effects of impact metamorphism in the sandstones are not merely to impoverish the cryptoendolithic habitat by pore collapse, but also to transform it from one suitable for cryptoendolithic colonists to one better suited for chasmoendolithic colonists. At the same time, the loss of these habitats can be caused by post-impact thermal annealing and recrystallization of melt phases. It follows that clasts within “cooler” impact ejecta and central uplift lithologies are likely to remain vesicular; whereas, clasts enclosed in hot, impact-melt bodies in the crater interior will likely recrystallize. At Haughton, the sediment-derived impact-melt breccias cooled very quickly so that many of these vesicular habitats were preserved (Osinski et al. 2005b), however, impact-melt layers generated from crystalline-rich targets remain at much higher temperatures for extended lengths of time (e.g., Grieve et al. 1977) so that the thermal annealing and recrystallization of vesicular clasts will be more likely.

The colonization patterns raise complications concerning the nomenclature of lithophytic organisms. “Cryptoendolithic” colonization has been defined as colonization of structural cavities within a rock, *sensu* Golubic et al. (1981). Chasmoendolithic organisms are defined as those associated with fissures and cracks (*sensu* Golubic et al. 1981). In heavily impact-shocked

rocks, fissures, fractures, internal cavities, and vesiculated areas of rock connected to the surface reduce to the same geologic manifestation. The lack of a clear distinction between “structural cavities” and “fissures and cracks” renders the separation between cryptoendolithic and chasmoendolithic colonization unclear. As the cells are not necessarily visible from the surface of such a rock (because in harsh environments the surface could be subject to high UV radiation, desiccation, etc., rendering it lifeless), the colonization within the irregular vesicles and impact fractures may, nevertheless, be “cryptic,” rendering the “cryptoendolithic” colonization observed in Fig. 3g to be an impact-induced “cryptic” subtype of chasmoendolithic colonization.

In general, our original hypothesis is supported by the observations reported here (Fig. 2). However, principally because of heterogeneities in shock effects, this simple interpretation does not fully describe the way in which impacts transform the characteristics of habitats. The scheme of shock level versus colonization potential (Fig. 5) shows that the collision of an asteroid or comet cannot merely be considered as another mechanism that either compresses or introduces fractures into rocks (similarly to tectonic activity or freeze-thaw, for example). Instead, well-defined suites of rocks are produced—the suitability for colonization is linked to the shock and thermal regimen produced in specific locations in and around an impact crater.

This work furthers our understanding of the effects of impact cratering on habitats for lithophytic microorganisms and the role of target lithology in defining the nature of the post-impact environment for a microbiota.

Acknowledgments—The samples described in this paper were obtained under the auspices of the NASA Haughton-Mars Project. We would like to thank Diane Johnson at the Planetary and Space Sciences Research Institute, Open University, for assistance with SEM. We thank the Culture Collection of Microorganisms from Extreme Environments (CCMEE) at the University of Rome “Tor Vergata” for provision of *Chroococcidiopsis* sp. 029.

Editorial Handling—Dr. Jens Ormö

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