



Effects of asteroid and comet impacts on habitats for lithophytic organisms—A synthesis

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Abstract—Asteroid and comet impacts can have a profound influence on the habitats available for lithophytic microorganisms. Using evidence from the Haughton impact structure, Nunavut, Canadian High Arctic, we describe the role of impacts in influencing the nature of the lithophytic ecological niche. Impact-induced increases in rock porosity and fracturing can result in the formation of cryptoendolithic habitats. In some cases and depending upon the target material, an increase in rock translucence can yield new habitats for photosynthetic cryptoendoliths. Chasmoendolithic habitats are associated with cracks and cavities connected to the surface of the rock and are commonly increased in abundance as a result of impact bulking. Chasmoendolithic habitats require less specific geological conditions than are required for cryptoendolithic habitats, and their formation is likely to be common to most impact events. Impact events are unlikely to have an influence on epilithic and hypolithic habitats except in rare cases, where, for example, the formation of impact glasses might yield new hypolithic habitats. We present a synthetic understanding of the influence of asteroid and comet impacts on the availability and characteristics of rocky habitats for microorganisms.

INTRODUCTION

Rocks offer a diversity of habitats to microorganisms and, although they might superficially appear to be similar, each habitat can experience different microclimatic conditions, and each habitat may host different colonists. Thus, it is of biological importance to distinguish between them.

To identify the different habitats, in this paper we follow the terminology of Golubic et al. (1981). Table 1 and Fig. 1 summarize the habitats with the names of the organisms that inhabit them.

The interior of rocks has merited particular attention in extreme deserts of the world as a potential habitat for microorganisms, on account of the ameliorated environmental conditions that are often found in these habitats compared with their surfaces (Friedmann 1980). Cryptoendolithic and chasmoendolithic organisms are not

limited to extreme environments. Endolithic attack of buildings is a matter of concern in many cities and towns (Sterflinger and Krumbein 1997). Nonetheless, in environments where the surfaces of rocks are exposed to extremes of temperature, UV radiation, and desiccation, the interior of rocks can be an important refugium for life.

The opportunities that rock interiors afford as an escape from environmental extremes has made them the subject of interest as possible locations for life on early Earth (Westall and Folk 2003) and more speculatively, on the surface of other planets (Wierzchos et al. 2003). The discovery of Precambrian endoliths, attributed specifically to euendolithic organisms (Campbell 1982), shows that lithic habitats have probably been important throughout the history of life on Earth.

The manner in which microorganisms colonize rocks is of profound importance for a number of fields of microbiology and earth sciences, as these microbial

Table 1. Habitats for lithophytic organisms and some of the effects of asteroid and comet impacts on their abundance and characteristics (nomenclature after that of Golubic et al. 1981).

Name of habitat	Description of habitat	Effects of impact at Haughton	General effects of impact ^a
Cryptoendolithic	Habitat within the interior of the rock	Increase in interconnected pore spaces in shocked gneiss and increase in translucence results in greater habitat availability.	Impact-induced fractures and pore space is likely to increase interior space for colonization in many rock types. However, photosynthetic endoliths require light penetration. Impact alteration of rock translucence may change availability of habitat.
Chasmoendolithic	Habitat in fissures and cracks within rock	Increase in habitats caused by fracturing of rocks. General to many rock types, characterized in dolomite.	Impact-induced fractures and fissures are likely to make an increase in chasmoendolithic habitat a common occurrence in impact structures. ^b
Euendolithic	Habitat formed by active boring/penetration by microorganisms	Euendolithic organisms not studied. However, habitat (carbonates) form immiscible melts with other target materials.	Increase in pore space caused by shock or changes in density of rock and rock chemistry (e.g., heterogeneous carbonate melts) could plausibly affect the ease with which microorganisms can actively penetrate into rocks.
Epilithic	Habitat on surface of rocks	No evidence for change in habitat availability.	The habitat on the surface of rocks will generally be unaffected by impact. However, two possible modes of change in suitability for colonization could be: 1) changes in weathering rates caused by mineralogical changes e.g., melting, could cause changes in the abundance of surface attachment sites (e.g., caused by changes in surface roughness); or 2) changes in macronutrient availability might change suitability of rock surfaces for microbial biofilm formation.
Hypolithic	Habitat on underside of rock	No evidence for change in habitat availability.	The habitat on the underside of rocks will generally be unaffected by impact. A possible instance in which hypolithic habitat availability could be changed would be alterations in the translucence of rocks (for example, the formation of impact glasses in desert settings), which would alter suitability of underside of rocks for photosynthetic hypoliths.

^aHabitat availability can be changed by, for example, the emplacement of a melt sheet (ejecta blanket) over previously available lithic habitats. The impact melt breccia hills of the Haughton impact structure cover Palaeozoic dolomite, which in other regions of Devon Island and the High Arctic provide abundant hypolithic habitat (Cockell and Stokes 2004). However, in this paper we focus on the direct effects on rocks caused by shock metamorphism.

^bCyanobacterial chasmoendoliths have recently been reported from shocked limestones in the Ries impact structure (Cockell et al. 2004).

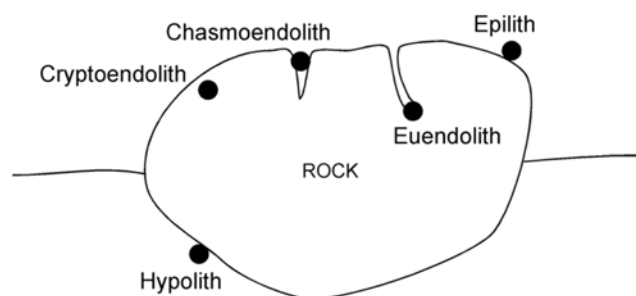


Fig. 1. Lithic habitats (see Table 1 for descriptions).

communities can influence weathering (Warscheid and Krumbein 1994) and rates of biogeochemical cycling (Johnston and Vestal 1989). Furthermore, discrete ecosystems can become established within rocks, allowing for elemental cycling and nutrient gradients, which benefit many different microorganisms (Friedmann 1982).

Asteroid and comet impacts generate pressures and temperatures that can vaporize, melt, shock metamorphose,

and/or deform a substantial volume of the pre-impact target sequence (e.g., Grieve and Pesonen 1992). This profound influence on target materials can change the availability and characteristics of habitats for lithophytic organisms (Cockell et al. 2002). As impact events are a universal phenomenon and would have been more frequent on the early Earth than today, understanding their influence on habitats for microorganisms is a fundamental objective in microbiology.

In this paper, we use data gathered at the Haughton impact structure, Nunavut, Canada, in combination with data from other craters to develop a synthetic understanding of the effects of impact on habitats for lithophytic organisms.

BIOLOGICAL CHARACTERISTICS OF THE FIELD SITE

The Haughton impact structure is located on Devon Island, Nunavut, Canadian High Arctic, and is centered at 75°22'N and 89°41'W. By geophysical criteria, the structure has an apparent diameter of about 24 km (Pohl et al. 1988),

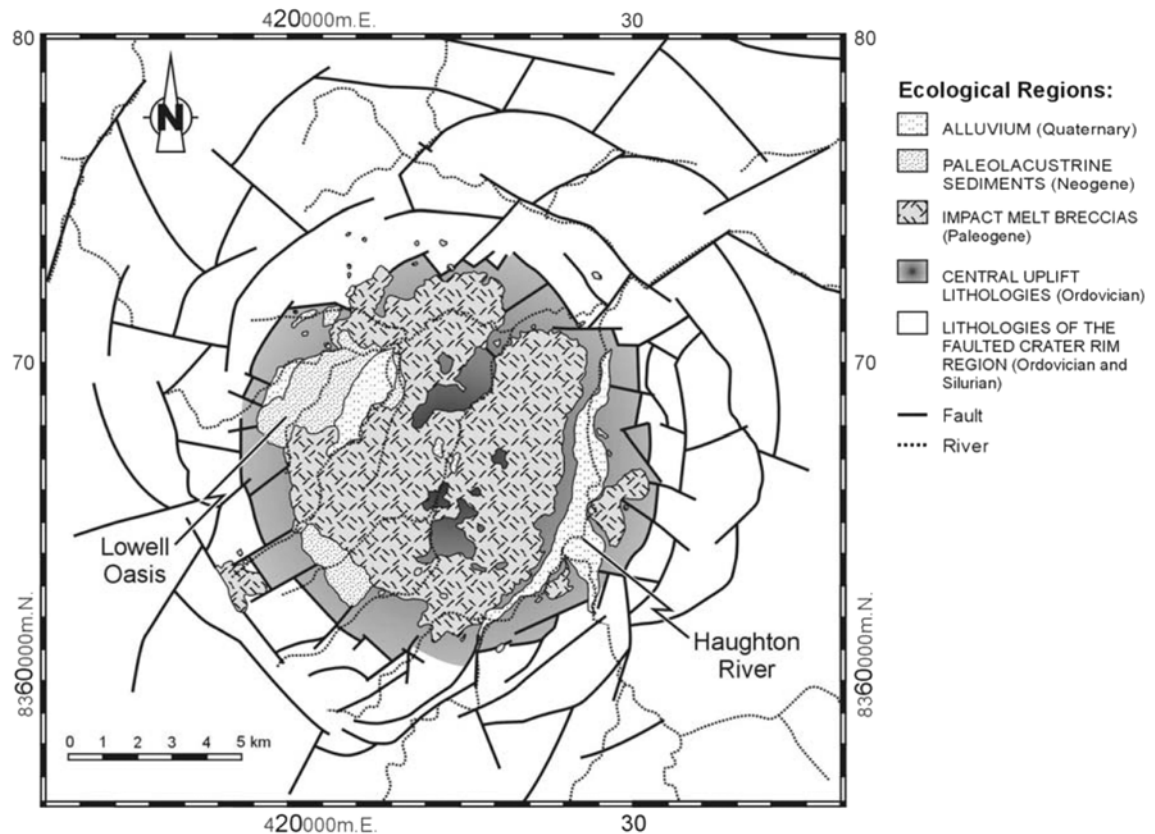


Fig. 2. A simplified map of the Haughton impact structure showing the main areas of ecological distinctiveness.

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 comprised of mostly carbonates (dolomite and limestone) overlying a basement of Precambrian granites and gneisses (Thorsteinsson and Mayr 1987; Osinski et al. 2005a). During the impact event, the crater was filled with an impact melt breccia deposit, a rubble-like mixture of target rocks dominated by carbonates (Figs. 2 and 3a) (Grieve 1988; Osinski and Spray 2001; Osinski et al. 2005b), which 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). This unit still covers most of the crater interior, a notable exception being a ~8 km² area in the west-central region of the structure, which is comprised of paleolacustrine deposits laid down within a lake (the Haughton Formation), which formed some time after the impact event (Frisch and Thorsteinsson 1978; Roberston and Sweeney 1983; Hickey et al. 1988; Whitlock and Dawson 1990; Osinski and Lee 2005), although it was certainly not formed immediately post-impact (see discussion in Osinski and Lee [2005]). 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 (Fig. 2).

Haughton crater and the region around it are situated in typical polar desert. In High Arctic polar deserts, vegetation cover is less than 5% and fauna depauperate compared to Low Arctic ecosystems (Babb and Bliss 1974; Bliss et al. 1984). This is the case for most of Devon Island, apart from localized regions such as the coastal Truelove Lowlands, in which biological productivity is substantially greater (Svoboda 1977). Similar to other sites on Devon Island (e.g., Walker and Peters 1977; Bliss et al. 1994), the soils of the Haughton region are primarily dolomitic and are nutrient poor. The low productivity of the soils is exacerbated by the climatic conditions. Devon Island lies within region IVa of Maxwell's (1981) climatic regions of the Canadian Arctic Archipelago and experiences a short growing season caused by short, cool summers.

Ecologically, the crater itself can be divided into several discrete regions (Figs. 2 and 3). The impact melt breccia hills have low vegetation cover, with generally less than 0.3% with localized increases to >2.5% in meltwater run-off channels (Fig. 3a) (Cockell et al. 2001). Higher vegetation covers are found on the alluvial terraces at the edges of the Haughton

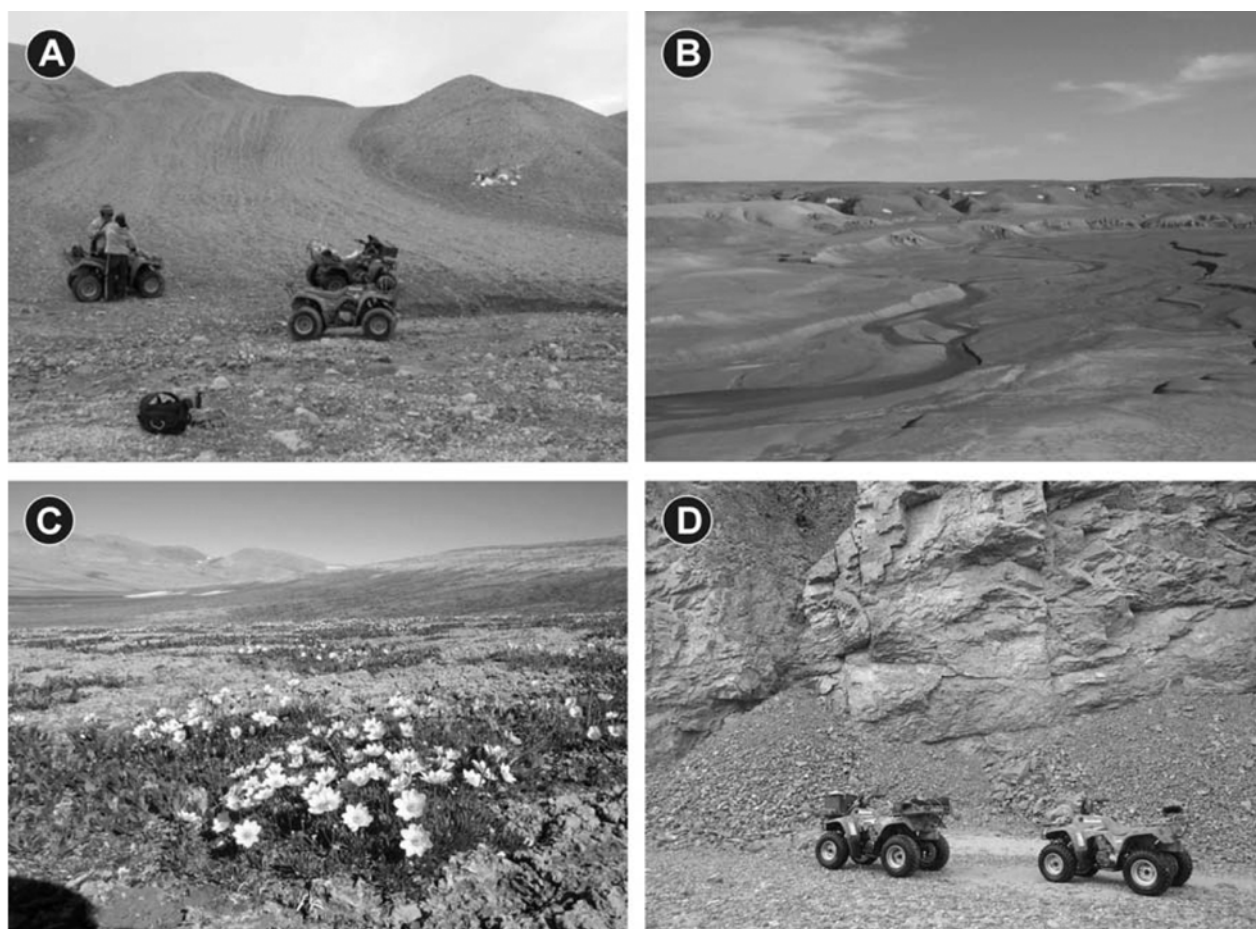


Fig. 3. Field photographs showing the different types of ecological regions within the Haughton impact structure. a) Impact melt breccias. All-terrain vehicles (ATVs) are shown in the foreground for scale. b) An image from a helicopter looking south down the Haughton River valley showing the alluvial terraces. c) Paleolacustrine sediments of the Haughton Formation are richly vegetated compared to other parts of the crater. d) Target rocks in the interior of the central uplift at Haughton are highly fractured and brecciated. ATVs are shown in the foreground for scale.

River, where covers can exceed 10% of the area in places, but generally they are closer to 2% (Fig. 3b). The paleolacustrine sediments of the Haughton Formation support a much richer ecology with vegetation cover in some areas greater than 80% (Fig. 3c). This impact-induced polar oasis is sustained by the rich organic content of the sediments, and possibly enhanced by their unconsolidated nature, and by water draining into the crater hydrologic depression (Cockell and Lee 2002). The Lowell Oasis supports arctic fox, hare, and musk ox during the summer months, and it is richly covered in lemming burrows. Within the crater are numerous ponds and lakes, whose limnological characteristics have been investigated (Lim and Douglas 2003). They are mainly alkaline, phosphorus-limited, ultra-oligotrophic (nutrient-poor) environments.

The lithic habitats discussed in this paper are localized to the impact melt breccia hills and the regions of dolomitic polar desert between them (Figs. 2 and 4). Outcrops within the paleolacustrine sediments are very sparse; this region of the crater is dominated by large areas of vegetation-covered soils.

CRYPTOENDOLITHIC HABITATS

Cryptoendolithic organisms live within the interstices of rocks, invading the pore spaces to reach the interior of the material. An increase in porosity caused by impact bulking and fracturing has been observed in many shocked rock lithologies in comparison to their unshocked forms (Table 2). However, a mere increase in porosity is not sufficient for creating cryptoendolithic habitats. The pore space must be interconnected in order to allow microorganisms to access the interior of the rock from the surface and allow them to spread within the rock matrix itself (e.g., Saiz-Jimenez et al. 1990). As impact bulking creates fractures and deformation features within target rocks, the increase in porosity is often accompanied by an increase in fracturing, which allows microorganisms to move within the rock matrix either by growth along surfaces or by water transport (Cockell et al. 2002).

At Haughton, we have observed an increase in porosity in impact-shocked gneiss (Cockell et al. 2002). The density

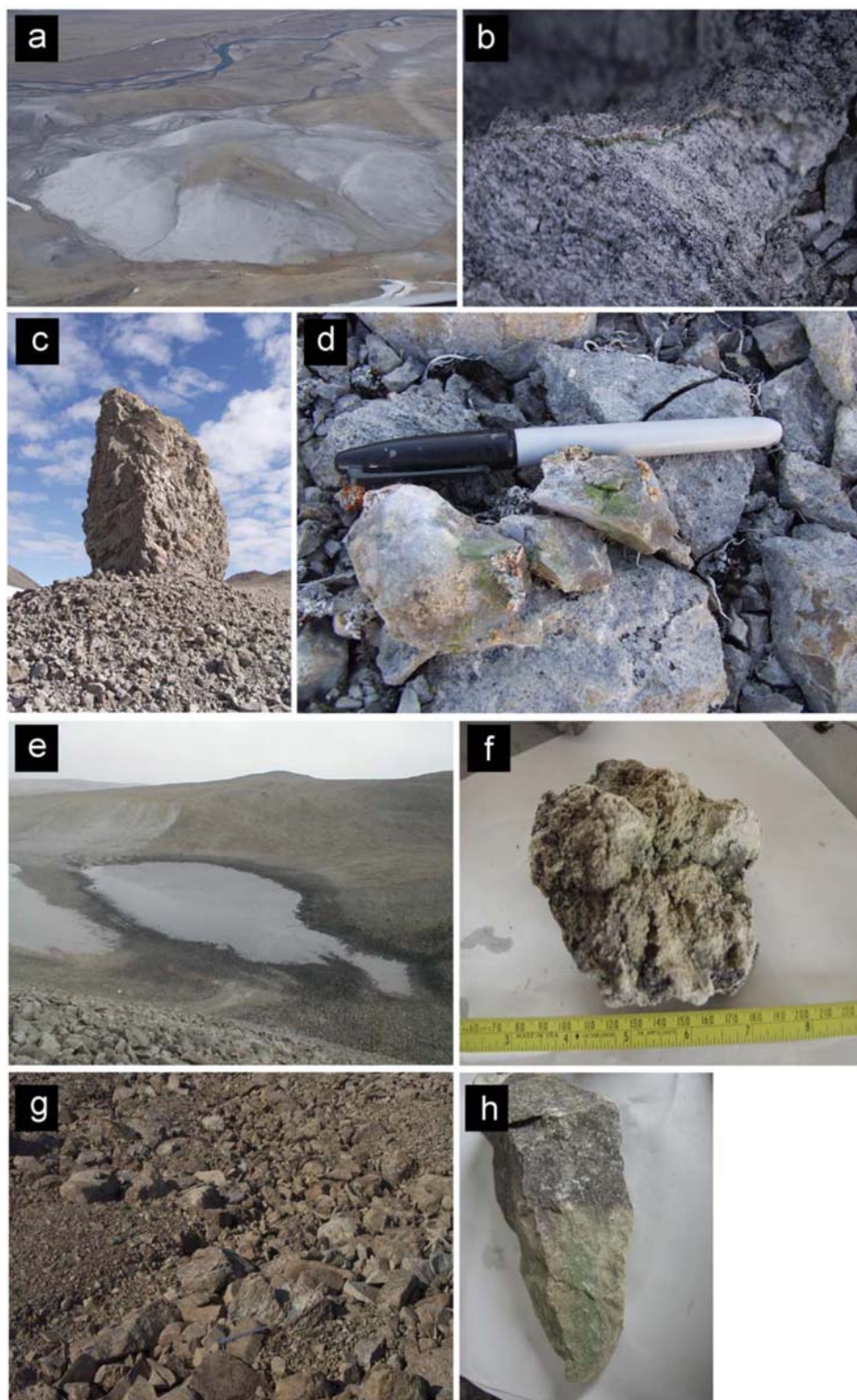


Fig 4. Lithophytic habitats in the Haughton impact structure. a) Melt-rock mound (~100 m in diameter). b) Cryptoendolithic colonization of shocked gneiss exposed on melt rocks evident as a layer of green in the rock (image is 10 cm across). c) Heavily impact-fractured dolomite block at 75°24.40'N, 89°49.89'W (circumference of block is 15.3 m). d) Cyanobacterial colonization of impact fractures within the dolomite block. e) Pond formed adjacent to melt-rock outcrop at 75°24.53'N, 89°49.77'W. Note the black ring around the pond that is caused by cyanobacterial epilithic colonization of rock surfaces (pond is ~8 m in width). f) Colonization of the surface of impact-shocked gneiss by cyanobacteria (black patches on rock). g) Typical sorted ground in dolomite on Devon Island at 75°25.19'N, 84°48.14'W (image is ~2 m across). h) Hypolithic colonization of sorted dolomite rocks evident as a green layer under the rock.

Table 2. Summary of published density and porosity data of impact structures.

Property	Impact rocks			Target rocks	
	Melt	Suevite	Breccia	Fractured	Unfractured
<i>Horizontal profiles</i>					
Bosumtwi ^a , D ~10.5 km; age ~1.07 Ma (Ghana)					
r_f/r_c	—	1.47	—	—	1.35
Density	—	2040	—	—	2510
Porosity	—	25.6	—	—	8.3
Ilyinets ^b , D ~8 km; age ~378 Ma (Ukraine)					
r_f/r_c	0.45	0.43	0.44	0.44	1.15
Density	2349	2113	2289	2462	2650
Porosity	5.7	15.4	11.1	5.2	1.1
Jänisjärvi ^c , D ~15 km; age ~700 Ma (Russia)					
r_f/r_c	0.4	0.3	0.4	0.3	1.69
Density	2569	2540	2536	2484	2775
Porosity	2.8	7.2	5.0	7.1	0.5
Karikkoselkä ^d , D ~2.4 km; age ~1.9 Ma (Finland)					
r_f/r_c	—	—	boulder	0.56	2.21
Density	—	—	2490	2637	2653
Porosity	—	—	7.2	1.5	1.3
Popigai ^e , D ~100 km; age ~35.7 Ma (Russia)					
r_f/r_c	0.72	0.71	—	—	0.74
Density	2522	1890	—	—	2775
Porosity	5.0	8.6	—	—	0.4
<i>Vertical profiles</i>					
Kärdla ^f , D ~4 km; age ~455 Ma, drill core (Estonia)					
r_f/r_c	—	0.26	—	1	—
Density	—	2390	—	2680	—
Porosity	—	9.3	—	1.35	—
Lappajärvi ^g , D ~23 km; age ~73.3 Ma, drill core (Finland)					
r_f/r_c	0.011	0.012	—	—	—
Density	2596	2297	—	—	—
Porosity	1.4	16.7	—	—	—
Suvasvesi N ^h , D ~4 km; age ~240 Ma, drill core (Finland)					
r_f/r_c	0.12	0.13	—	—	1.07 ^j
Density	2369	2427	—	—	2804 ^j
Porosity	14.8	9.7	—	—	0.6 ⁱ
Sääksjärvi ⁱ , D ~6 km; age ~600 Ma, drill core (Finland)					
r_f/r_c	—	—	—	—	—
Density	—	2280	2170	2343	2597
Porosity	—	15.1	19.9	13.0	6.6
Mean N = 9					
Density	2481	2247	2371	2521	2685
Porosity	5.9	13.5	10.8	5.6	2.7
Trend		Density increases and porosity decreases			

r_f/r_c is the normalized distance, where r_f is the distance from the structure's center and r_c is radius of the structure; D is diameter of the structure; density (kgm^{-3}) is generally bulk density in laboratory conditions; porosity (%) is measured using Archimedeian principle (e.g., Kivekäs 1993). ^jLateral sampling on the surface.

^aPlado et al. 2000. ^bPesonen et al. 2004. ^cSalminen 2004. ^dPesonen et al. 1999. ^eSalminen, unpublished data. ^fPlado et al. 1996. ^gKukkonen et al. 1992. ^hWerner et al. 2002. ⁱKivekäs 1993. Note that the porosity of impact melt breccias from Haughton crater, measured using the Archimedeian principle (Pesonen, this work; see Pesonen et al. 2004 for discussion), was determined as $31.4 \pm 2.4\%$ (mean of 6 samples), the porosity of impact-shocked gneiss (~20–40 GPa shock pressures) was measured as $18.3 \pm 2.3\%$, and the porosity of unshocked rocks was measured as $9.3 \pm 1.2\%$. All samples were obtained at melt rock hill adjacent to $75^\circ 24.53'N$, $89^\circ 49.77'W$.

and porosity of shocked rocks (shocked to >20 GPa) is on the order of $1 \times 10^3 \text{ kgm}^{-3}$ and 18.3%, respectively (Table 2). The low-shocked or unshocked rocks have a more typical density and porosity of $>2.5 \times 10^3 \text{ kgm}^{-3}$ and 9.3%, respectively.

The volatilization of opaque minerals and the formation of fractures within the rock matrix increases the translucence of the shocked gneiss. Penetration of light at 680 nm, the chlorophyll *a* absorption maximum, is increased by about an order of magnitude (Cockell et al. 2002) compared to unshocked rocks. If the minimum light for photosynthesis is taken to be 20 nmol/m²/s (Raven et al. 2000), then this corresponds to a depth of approximately 3.6 mm in the shocked material, but about 1 mm in the low-shocked material. This latter depth prevents the cyanobacteria from colonizing the interior of the unshocked rock except within the weathering crust, where rare chasmoendolithic colonization is observed. The porosity of the unshocked rocks is also insufficient for cyanobacterial cryptoendolithic colonization. In the shocked material, coherent bands of cryptoendolithic colonization at depths typically ~1–5 mm can be found (Figs. 4a and 4b).

The interconnected fractures within the shocked material provide a habitat suitable for a wide diversity of non-photosynthetic heterotrophic (organic-using) microorganisms (Fike et al. 2003). These microorganisms are similar to those found in soils and ices elsewhere in polar regions, and they probably leach into the rock from the soils in seasonal snow melt or rain, and subsequently form biofilms within the rock matrix.

The interior of the shocked rocks provides protection from environmental stress(es). Within the rock, temperatures during the summer months are often higher than the air temperature, sometimes by up to 10 °C (Cockell et al. 2003a). After short rain falls, moisture becomes trapped within the pore spaces of the shocked rocks, providing water for the organisms after the surface has dried in the wind. The interior of the rocks also protects against UV radiation damage (Cockell et al. 2002).

The cryptoendolithic photosynthetic organisms found within the Haughton gneiss demonstrate impact-induced formation of cryptoendolithic habitats, but more specifically, they demonstrate how shock metamorphism can yield cryptoendolithic habitats in non-sedimentary lithologies, which are otherwise unusual. Endolithic colonization of non-sedimentary rocks has been reported in weathering crusts and cracks in granite, manifested as chasmoendolithic colonization (e.g. Friedmann 1977; De los Rios et al. 2005). However, the best characterized photosynthetic cryptoendolithic habitats are those associated with sandstones and limestones (e.g., Friedmann 1982; Saiz-Jimenez et al. 1990; Bell 1993; Wessels and Büdel 1995). Sedimentary rocks such as these are sufficiently translucent and porous for cryptoendolithic colonization.

The process of shock metamorphism is thus not merely

about increasing the porosity and translucence of non-sedimentary rocks for photosynthetic cryptoendolithic colonists, but it involves creating conditions for colonization in non-sedimentary rocks, which would not have been previously available.

Impact events generate new lithologies (e.g., impact breccias and melt rocks) that can be more porous than the pre-impact target rocks, and at least have sufficient porosity for colonization. For example, surficial or fallout suevites at the Ries impact structure, Germany, typically have porosities of ~5–15 vol% (Osinski et al. 2004). We have shown how the breccias and melt rocks of the Haughton structure are sufficiently porous to sustain heterotrophic microbial populations (Fike et al. 2003). Thus, the interior of melt rocks can host diverse assemblages or communities of non-photosynthetic microorganisms. Although these organisms do not form the highly structured layered communities typically associated with photosynthetic cryptoendolithic communities, they are nevertheless lithophytic organisms associated with high porosities generated in impact-altered target materials.

CHASMOENDOLITHIC HABITATS

Chasmoendolithic organisms depend upon macroscopic cracks and fissures in rocks as a habitat. The most widely characterized chasmoendoliths are cyanobacterial colonists (Büdel and Wessels 1991; Broady 1979, 1981a). Chasmoendolithic habitats have particular importance in polar regions for the same reasons as those described for cryptoendoliths (Broady 1981a). The interior of the cracks and fissures provides escape from desiccation, rapid temperature variations, and UV radiation. Unlike cryptoendolithic habitats, chasmoendolithic habitats can be formed in potentially any substrate. Provided that the substrate is not toxic, then any macroscopic cracks can provide surfaces for growth. Unlike cryptoendolithic habitats, photosynthetic organisms do not require that the substrate is translucent, because light penetrates from the surface directly into the cracks in the substrate.

In the Haughton structure, cyanobacterial chasmoendolithic communities are evident in impact-shattered dolomites (Cockell and Lim 2005). In particular, large regions of the central uplift are highly fractured, faulted, and brecciated (Fig. 3d), as well as several large ejecta blocks (Figs. 4c and 4d). Coccoid cyanobacterial colonists, with *Gloeocapsa*-like and *Chroococcidiopsis*-like morphology have invaded the substrate along fracture planes. Similar colonization is not observed in unshocked dolomitic erratics found outside the crater.

Shattered limestones from the Ries crater in Germany are also found to harbor cyanobacterial chasmoendolithic communities (Cockell et al. 2004). Similarly to Haughton, the organisms invade the fracture planes.

Impact-induced fracturing is common to all impact events and so the simplest statement that can be made concerning the effects of impact on the chasmoendolithic habitat is that shock metamorphism can increase the abundance of habitats. These habitats may form in the subsurface as well as the surface, but at the surface, where photosynthetically active radiation is available, impact-induced chasmoendolithic habitats will then provide a habitat for photosynthetic pioneers. These habitats will be particularly important in the fractured and faulted central uplifts and uplift rings of complex impact structures.

AN INCREASE IN CHASMOENDOLITHIC AND CRYPTOENDOLITHIC HABITATS IS LIKELY TO BE A COMMON EFFECT OF IMPACT

The most microbiologically important effect of impact is bulking—increasing the porosity of rocks and the abundance of interconnected fractures. As lithophytic microorganisms require surfaces on which to grow, an increase in porosity and fracturing can increase the availability of surfaces for microbial growth. However, as organisms might be nutrient-limited, it is not necessarily the case that an increase in surface area for growth will be correlated to an increase in biomass. Thus, it is important to understand that the effect of impact is to increase the potential for growth, specifically with respect to surface area for biofilm formation.

It is well-known that densities of impact rocks can be up to 30% lower than in unshocked target rocks due to impact-increased porosity and fracturing (Pesonen et al. 1999; Henkel 1992; Pilkington and Grieve 1992; Plado et al. 1996). In some cases, natural shock-induced fracturing has been accurately replicated in laboratory shock experiments, providing a quantitative understanding of the process, such as, for example, in the case of shocked basalts from the Lonar crater, India (Kieffer et al. 1976a). These collected observations suggest that chasmoendolithic and cryptoendolithic habitat formation are common to impact cratering, and common to many different lithologies.

Several craters either directly or indirectly demonstrate that shock metamorphism causes an increase in the potential accessibility of target lithologies to a microbiota. Calculated shock determinations based on mineralogy are available for the Charlevoix impact structure, Quebec ($D = 54$ km, age ~ 342 Ma) (Grieve et al. 1990). This example (Fig. 5a) illustrates the radial (in this case horizontally) decay of shock from the centre of the structure (close to the point of impact). The observed rate of recorded shock pressure attenuation is almost exponential from about 20 GPa near the center to about 4 GPa at 10 km distance from the center and up to the rim. Unfortunately, no porosity determinations are available.

Figure 5b shows the decay of fracture density as a function of distance for the Elgygytgyn structure, Russia ($D =$

18 km, age = 3.5 Ma) (Gurov and Gurova 1983). We note that the fracture density decreases exponentially away from the impact centre. The effectiveness of shock metamorphism at opening pore space and increasing the abundance of fractures is reflected in the data of electrical conductivity in and around the Siljan impact structure, Sweden, where conductivity diminishes outwards from the centre of the structure (Fig. 5d) (Henkel 1992). The increasing electrical conductivity into the centre of Siljan is proposed to be caused by the presence of saline fluids in pores and fractures; an indirect demonstration of impact-induced fracturing.

Table 2 summarizes the porosity data of nine impact structures. The rocks have been divided into two categories: impactites (divided into melts, suevites, and breccias) and target rocks (divided into fractured and unfractured). These units roughly correspond to the increasing distance either downward (drill core data) or radially away (lateral sampling) from the point of impact. However, the distances (r_i/r_c) are to be viewed only as rough measures of the original radial distance since the structures are different in their diameter, age, erosional level, and tectonic modification. Nevertheless, we note that generally the porosity decreases when moving away from impactites to fractured and to unfractured target rocks. For example, in the case of the Jänisjärvi impact structure (Fig. 5c) (Salminen 2004) the porosity has a trend to decrease (from approximately 10%) in impactites to the unfractured target rocks (approximately 0.5%) (Fig. 5c), consistent with decreasing shock pressure.

The higher porosity observed in the subsurface of impact structures compared to their exteriors (Table 2) shows that impact events could potentially render the subsurface more amenable to colonization by microbiota as well as their surface habitats. However, the biomass of subsurface biota appears to be correlated to availability of redox couples, rather than availability of pore or fracture space (Wellsbury et al. 1997; D'Hondt et al. 2004; Parkes et al. 2005), and so although impact-induced fracturing might increase the ease with which biota can colonize rocks, it is not necessarily the case that fracturing in the deep subsurface would provide significant advantages to a nutrient-limited biota. On the other hand, the fracturing of rock could potentially enhance the supply of electron donors and acceptors, examples being the fracturing of basalts to yield hydrogen, whereby ferromagnesium silicates reduce water, a process which has been demonstrated using crushed basalt in the laboratory, albeit at quite narrow pH ranges (Anderson et al. 1998), or the fracturing of iron-rich rocks to yield new sources of reduced or oxidized iron for iron-utilizing microorganisms. However, these transient availabilities of energy supplies may be irrelevant in regions sterilized by the thermal pulse from the impact, or they may be too short-lived to be useful over geological time scales (Anderson et al. 1998).

Impact events can alter the oxidation state of metals; geochemical studies show that the conditions of impact may

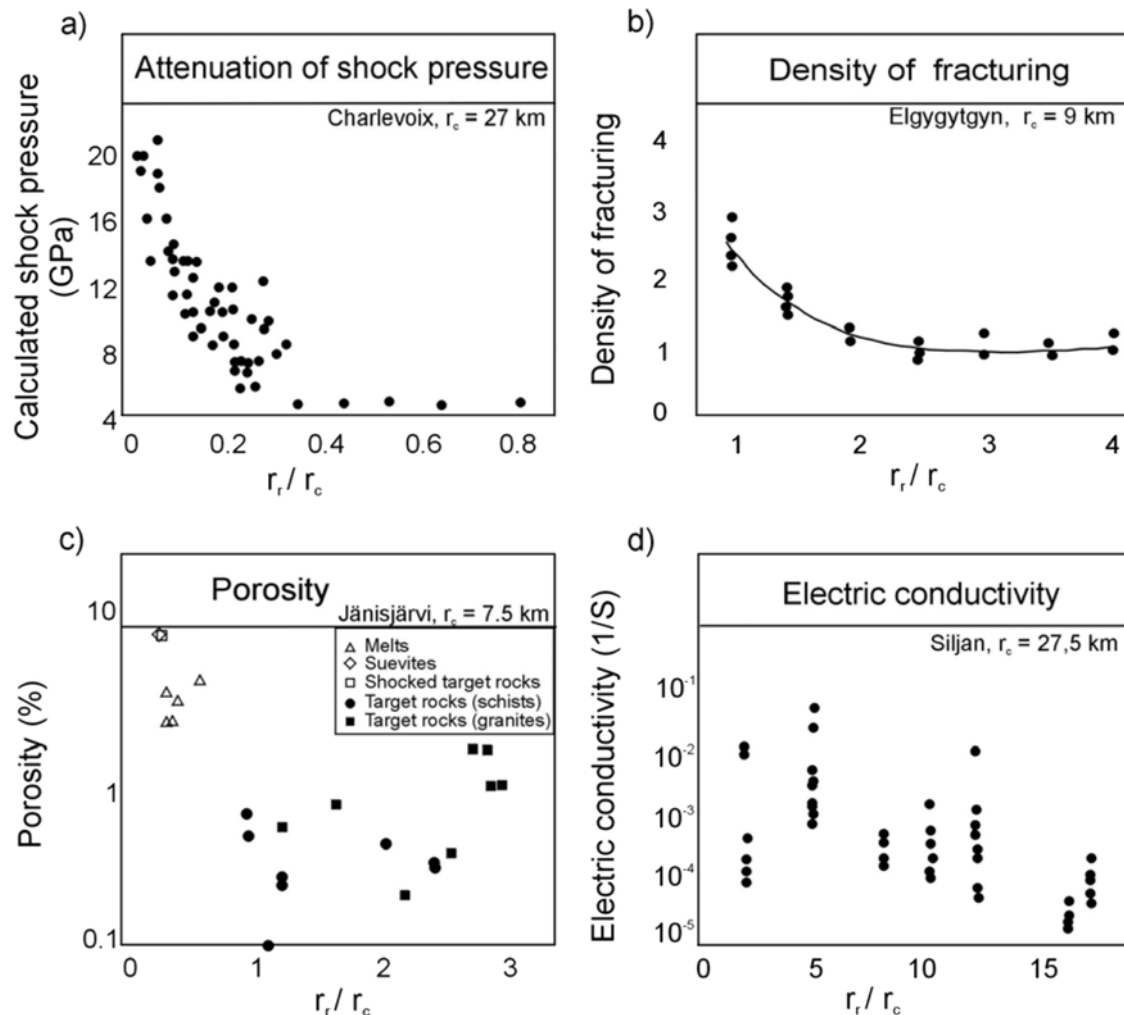


Fig 5. Some physical properties of impact structures as a function of the horizontal distance from the structure's center point (r_r/r_c is the normalized distance, where r_r is the distance from the structure's center and r_c is radius of the structure). a) Calculated shock pressure in Charlevoix structure (after Grieve et al. 1990); b) density of fracturing in Elgygytgyn structure (after Gurov and Gurova 1983); c) porosity of the Jänisjärvi structure (Salminen 2004); d) electrical conductivity of the Siljan structure (modified after Henkel 1992).

be reducing, evidenced by low ferric iron to ferrous iron ratios in tektites (Koeberl 2004). This process could potentially alter the bioavailability of redox couples and nutrients in post-impact lithophytic habitats, both at the surface and in the subsurface.

Other subtleties must be understood when formulating a synthetic understanding of the role of impact in influencing lithophytic habitats. First, lithology does play a role in the nature of the post-impact lithophytic habitat. In the case of sedimentary lithologies with high porosities, some of the energy delivered in impact causes pore collapse, thus reducing porosity. Kieffer and co-workers showed that in the Coconino sandstones at Meteor crater, Arizona, the porosity of the material was reduced from approximately 20% (Kieffer 1975) to less than 5% (Kieffer 1971) following low shock pressures. Thus, in some cases, impact will reduce pore space available for endolithic colonization in rocks that were very

porous prior to impact. The reduction in porosity was caused by the re-orientation of the grains into a more closely packed configuration. At high shock pressures (although still <25 GPa) the grains become highly fractured and deformed, eventually plastically flowing around each other (Kieffer 1971). Hot material is "jetted" into pore spaces (Kieffer et al. 1976b). The density of the shocked Coconino samples was not reduced to the intrinsic density of the material. The remaining porosity within the shocked material was accounted for by the space between the re-oriented grains or the fractured rocks. In the case of heavily fractured rocks, the habitat may be partly held together by the interlocking fragments of shocked rock rather than the arrangement of separate grains. We would predict that in some high porosity lithologies, impact shock will reduce bulk porosity and impede colonization. However, concomitantly, by fracturing the rock and its component grains, thus increasing surface

area and potentially the interconnectedness of the interior rock space, the effects of the reduction of bulk porosity could be partly mitigated.

Second, intense shock lithification can cause melting of the material and the formation of glass. Glass formation has been observed in many shocked lithologies, for example, in the basalts and sandstones discussed earlier (Kieffer 1976a, 1976b). In these two cases, glass formation was observed at shock pressures >50 GPa. Glass within the Coconino sandstone was found to form continuous ribbons around quartz grains and it filled the intergrain spaces. Although many of these glasses were found to have a microscopic structure that was irregular, patches of homogeneous glass formation in the interstices of the rock could impede potential colonists.

Although there are complexities to the impact-induced formation of lithophytic habitats that are determined by shock pressures, lithology, and nutrient availability, it is evident that geologic changes, such as shock metamorphism and fracturing, result in some changes in biological potential that are common to all impact events, the most important being an increase in fractures for potential chasmoendolithic and cryptoendolithic colonists.

EUENDOLITHIC HABITATS

We have not undertaken a study of euendolithic organisms within the crater, but we have studied the euendolithic habitat. The most common habitat for euendoliths, which actively bore into rock, is in carbonate lithologies (Hoppert et al. 2004). The most investigated genus of euendolithic cyanobacteria is *Hyella*. Corals provide a source of biogenic carbonates and have been a previous focus of study on euendolithic organisms (Le Campion-Alsumard et al. 1995; Tribollet and Payri 2001). Carbonates are readily dissolved by organic acids produced by euendoliths, allowing them to bore into the substrate (Fig. 1). Similarly to the crypto- and chasmoendolithic habitat, the euendolithic habitat provides protection from environmental extremes.

Carbonates are present in the target rocks of approximately one-third of the world's known impact structures. Despite the many uncertainties regarding the response of carbonates to impact, it is commonly accepted that these lithologies decompose after pressure release due to high residual temperatures (e.g., Agrinier et al. 2001). Thus, one effect of impact on the euendolithic habitat is simply to vaporize it. However, recent studies suggest that the dominant process is melting, and not decomposition (e.g., Graup 1999; Jones et al. 2000; Osinski and Spray 2001), a view supported by the phase relations of CaCO_3 (Ivanov and Deutsch 2002). At Haughton, the carbonate melts are mixed with other melt phases, including sulfate minerals and impact glasses (Osinski and Spray 2001, 2003; Osinski et al. 2005b). The melt phases are mixed on micrometer to millimeter scales,

and the mixing of the carbonates with other target lithologies results in a physically and chemically heterogeneous substrate. These substrates would be expected to be more difficult to bore than unaltered carbonates, as euendolithic bore holes are more likely to encounter other melt phases or clasts of target materials that do not readily lend themselves to dissolution by organic acids, such as sulfates in the case of the Haughton structure.

Thus, we would expect the formation of heterogeneous melts and inclusion of unmelted clasts to impede penetration of euendoliths into impact melt breccias/rocks, depending on the degree of melting and the exact composition of the target lithologies. Conversely, however, increases in porosity by impact bulking might be predicted to render some carbonate rocks more amenable to euendolithic colonization, and to offer a greater surface area for initial attachment and colonization in analogy to post-impact chasmoendolithic colonization. The carbonate lithologies in the central uplift at Haughton are highly fractured and brecciated (Fig 3).

In addition to carbonate lithologies, euendolithic borings have been found in basaltic glasses (e.g., Thorseth et al. 1992; Fisk et al. 1998). The organisms within these glasses are preferentially found at the margins of glasses, where access to the substrate and possibly nutrient supplies are available. Impact melt glasses formed at high shock pressures and emplaced within the target lithology offer similar potential microhabitats for euendolithic glass-boring colonists.

EPILITHIC HABITATS

The surface of rocks, which provide a stable surface on which biofilms can develop, provide a habitat for an extraordinary diversity of microorganisms. Some of these rock surface biofilms, particularly in the world's hot deserts, form distinctive desert "varnishes" and crusts (e.g., Kurtz and Netoff 2001; Perry et al. 2003). At Haughton, cryptogamic crusts are abundant, particularly in areas where seasonal meltwater water is channeled. These crusts are primarily formed from diverse cyanobacterial assemblages, including *Nostoc* spp., *Gloeocapsa* spp. and filamentous cyanobacteria such as *Phormidium* and *Scytonema*, and they can also contain lichens and mosses in more luxuriant stands. Cyanobacterial epiliths have been observed on and within gypsum outcrops in Haughton (Parnell et al. 2004). Cryptogamic epilithic crusts and cyanobacterial mats are widespread in the arctic, and have been reported from a number of locations (e.g., Gold and Bliss 1995; Quesada et al. 1999; Dickson 2000). We have not observed any effect of impact metamorphism on epilithic colonization. Around transient meltwater streams and in topographic lows, impact altered clasts, such as gneiss, provide surfaces for epilithic colonization, similarly to nearby locations outside the crater on Devon Island (Figs. 4e and 4f). We have observed lower vegetation covers on the top of the impact melt breccia hills at

Haughton compared to the alluvial terraces at the edges of the Haughton River, and compared to other locations that have been studied on Devon Island (Cockell et al. 2001), but we attributed this to desiccation experienced on the top of the high, exposed hills, rather than to impact alteration of the rocks themselves.

As epilithic organisms will colonize any surface where adequate nutrients and water are available, there is no obvious mechanism by which impact metamorphism would directly alter the epilithic habitat, except by changing the chemistry of the rocks, and thus the potential source of nutrients or redox couples for surface-attached organisms. As discussed earlier, the reduction of metals during the impact process (e.g., Koeberl 2004) is one such mechanism by which potential surface chemolithotrophic redox couples could be influenced.

The epilithic habitat might well be impoverished immediately after impact, however, when volatilization of biologically important nutrients such as phosphorus and nitrogen compounds is likely to have occurred. Since the major biologically important nutrients volatilize at temperatures well below those associated with region affected by impact shock heating (Cockell et al. 2003b), then the surfaces of rocks are likely to be rendered nutrient poor. Following impact, nitrogen fixation, phosphorus input from rain and animals, and input of other compounds and trace elements are likely to reduce the chemical differences between the epilithic habitat inside the crater compared to outside.

HYPOLITHIC HABITATS

The underside of rocks provides a surface for biofilms of both photosynthetic and non-photosynthetic organisms (e.g., Smith et al. 2000). In the case of photosynthetic organisms, they have the requirement for light as a source of energy and, therefore, hypolithic colonization usually requires that the rock is translucent. For this reason, most hypoliths to date have been reported under quartz-dominated lithologies (Vogel 1955; Cameron and Blank 1965; Broady 1981b; Schlesinger et al. 2003), which can have sufficient translucence for light to penetrate directly through the rock to the microbiota underneath (Berner and Evenari 1978).

We have not observed any influence of impact metamorphism on hypolithic colonization at Haughton. Shocked clasts exposed on the surface of the Haughton melt hills are colonized on their underside by cyanobacterial assemblages, similarly to dolomitic rocks outside the crater. These hypoliths are dominated by *Gloeocapsa* (cf. *atrata* Kützing), *Gloeocapsa* (cf. *punctata* Nägeli), *Gloeocapsa* (cf. *kuetzingiana* Nägeli), *Aphanothece* and *Aphanocapsa*-like cells and *Chroococciopsis*-like cells (Cockell et al. 2002; Cockell and Stokes 2004). Various filamentous forms have been observed, primarily *Oscillatoriales*, similar to *Leptolyngbya* and *Scytonema*. Unicellular algal chlorophytes were observed.

Hypolithic colonization is widespread in the polar desert of the Canadian High Arctic (Figs. 4g and 4h). We hypothesize that this is caused by cyclical freeze-thaw that results in openings around the edges of opaque stones into which light can penetrate, rather than the translucence of the rocks themselves (Cockell and Stokes 2004). In some areas, over 90% of rocks are colonized on their underside. Thus, although the translucence of the shocked gneiss is greater than that of low or unshocked gneiss, hypolithic colonization of these rocks is not related to impact metamorphism. Indeed, the shocked gneiss is still insufficiently translucent to allow adequate light to penetrate for photosynthesis, even under a thickness of 1 cm.

An instance in which impact metamorphism might increase the abundance of hypolithic habitats is when impact glasses are formed in sandy deserts, or in sandstone lithologies. The colonization of the underside of impact-generated translucent melt-rocks and glasses would present an example of impact-enhanced hypolithic colonization. It was noted in the field in an expedition to the Libyan Desert Glass (LDG) strewn field in southwest Egypt (see Koeberl et al. 2003 for a first report) that in many cases larger LDG samples (10 cm and above), which had been in situ in the sand for a long time (smaller pieces are easily transported by wind during sandstorms), are corroded on their underside. In these cases there was often a thin soil layer attached to the rough underside of the glass, and in many cases green crusts of phototrophic communities were observed.

Conversely, impact metamorphism of quartz could even render a pre-impact hypolithic habitat (and a quartz cryptoendolithic habitat) less suitable for microbial colonization if the quartz becomes opaque. "Toasted" quartz has been reported to be more opaque than unshocked material. This was primarily attributed to the presence of fluid inclusions along planar deformation features (Whitehead et al. 2002). Kieffer et al. (1976b) describe the formation of amorphous "froth" within shocked Coconino sandstones near high-pressure phase regions, which they attribute to the violent separation of vaporized water and silica. The high porosity vesicular material causes an increase in light scattering, and thus opacity. They have also observed opaque glasses that surround grains in highly shocked material. The reduction of light penetration through "froth," "toasted," and glassy materials illustrates how impact metamorphism can alter lithophytic habitats in ways that specifically influence potential colonization by photosynthetic microorganisms.

SUMMARY AND CONCLUSIONS

Asteroid and comet impacts cause profound changes to target rocks, which can influence the availability of habitats for microorganisms.

For epilithic and hypolithic organisms, these effects are generally not important because they grow on the outside

surfaces of rocks, where rock porosity is not a factor in growth. Except where shock metamorphism alters the translucence of rock, thus altering the habitat for photosynthetic hypolithic colonists, or where the chemistry of the rock is sufficiently altered to influence surface colonization, hypolithic and epilithic habitats are largely unaltered by impact. Of course, melt rocks and ejecta blankets might well cover pre-existing lithophytic habitats, thus rendering them unsuitable for colonization, for example by photosynthetic organisms, but here we are concerned with the direct effects on the target lithology.

The availability of chasmoendolithic habitats can be increased by the process of shock-induced fracturing and bulking of target rocks, which increases the number of macroscopic cracks that are accessible from the surface of the rock by pioneer organisms. As macroscopic cracks do not require any special geological attributes of the rock (e.g., composition, density, porosity), impact-induced chasmoendolithic habitat formation is probably the most common effect of impact on the availability of habitats for lithophytic organisms.

Unlike chasmoendolithic colonization, the requirement for interconnected pore spaces for access to the subsurface and subsequent spread of biofilms within the rock interior imposes more specific geological requirements for the formation of cryptoendolithic habitats. Photosynthetic cryptoendoliths not only require interior interconnected pore space, but also sufficient translucence for light to penetrate into the rock. We have shown how impact-altered gneiss in the Haughton structure becomes more translucent as a result of shock metamorphism. This process is not necessarily common. The “toasting” of some target materials may even render them more opaque. The requirement for both an increase in interconnected pore spaces and translucence makes the impact-formation of cryptoendolithic habitats for photosynthetic organisms in non-sedimentary lithologies a particularly remarkable, and perhaps unusual, effect of impact on the habitat for lithophytic organisms.

In summary, this work has revealed the effects of asteroid and comet impacts on the habitat for lithophytic organisms. An investigation of other impact craters will refine our understanding of these processes and the variations in their manifestation. This synthesis suggests that impact cratering must be viewed as a truly biologic process, as well as a geologic one (Melosh 1989).

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