

The biology of impact craters – a review

CHARLES S. COCKELL^{1*} and PASCAL LEE²

¹British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK

²SETI Institute and NASA Ames Research Center, MS 245-3, Moffett Field, CA 94035-1000, USA

(Received 7 March 2001; revised 9 October 2001; accepted 10 October 2001)

ABSTRACT

Impact craters contain ecosystems that are often very different from the ecosystems that surround them. On Earth over 150 impact craters have been identified in a wide diversity of biomes. All natural events that can cause localized disruption of ecosystems have quite distinct patterns of recovery. Impact events are unique in that they are the only extraterrestrial mechanism capable of disrupting an ecosystem locally in space and time. Thus, elucidating the chronological sequence of change at the sites of impacts is of ecological interest. In this synthetic review we use the existing literature, coupled with our own observations at the Haughton impact structure, Devon Island, Nunavut, Canada to consider the patterns of biological recovery at the site of impact craters and the ecological characteristics of impact craters. Three phases of recovery are suggested. The Phase of Thermal Biology, a phase associated with the localized, ephemeral thermal anomaly generated by an impact event. The Phase of Impact Succession and Climax, a phase marked by multiple primary and secondary succession events both in the aquatic realm (impact crater-lakes) and terrestrial realm (colonization of paleolacustrine deposits and impact-generated substrata) that are followed by periods of climax ecology. In the case of large-scale impact events ($> 10^4$ Mt), this latter phase may also be influenced by successional changes in the global environment. Finally, during the Phase of Ecological Assimilation, the disappearance of the surface geological expression of an impact structure results in a concomitant loss of ecological distinctiveness. In extreme cases, the impact structure is buried. Impact succession displays similarities and differences to succession following other agents of ecological disturbance, particularly volcanism.

Key words: Impact crater, succession, lake, hydrothermal, Mars, Haughton, comet, asteroid.

CONTENTS

I. Introduction – the significance of impact crater biology	280
II. Identifying common patterns in post-impact biological changes.....	283
(1) Existing studies.....	283
(2) The Haughton impact structure.....	283
III. The chronological sequence of post-impact ecology.....	287
(1) Phase of Thermal Biology	287
(a) Physical constraints.....	287
(b) Hydrothermal biology	288
(c) Planetary and exobiological significance.....	290
(2) Phase of Impact Succession and Climax	291
(a) The impact crater-lake	291
(i) Impact crater-lake arrangements.....	291
(ii) Microbial profiles of impact crater-lakes.....	291
(iii) Impact crater-lakes and the significance of their paleobiological record	294
(iv) Intracrater-lake biology and the potential exobiological relevance.....	295

* Corresponding author: Charles S. Cockell, British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK. Tel: 01223 221560; Fax: 01223 411722; e-mail: cscoc@bas.ac.uk

- (b) Recolonization on land..... 296
 - (i) The hydrologic impact oasis 296
 - (ii) Recolonization on a paleolacustrine substratum 296
 - (iii) The salt pan oasis..... 297
 - (iv) Recolonization on impact-generated and other non-lacustrine substrata..... 297
 - (v) Climax ecology 301
 - (vi) Impact-induced fertilization?..... 301
- (c) The ecotone surrounding the impact site..... 302
- (d) Recolonization and succession in pelagic impact events 302
- (e) Dependence on geological epoch 302
- (f) Recolonization after changes in the global environment..... 303
- (g) The impact crater as a biogeographical island 303
- (h) Human interactions – an unusual type of recolonization and succession event..... 304
- (3) Phase of Ecological Assimilation 305
- IV. Conclusions..... 307
- V. Acknowledgements 307
- VI. References..... 307

I. INTRODUCTION – THE SIGNIFICANCE OF IMPACT CRATER BIOLOGY

Impact events can be regarded as biologically ‘resetting’ events because they render the immediate area of the impact sterile as a result of the intense heat (up to approximately 15000 K) and pressures (several hundred GPa) reached at the point of contact of the impactor with the target planet (Melosh, 1989). Large-scale impacts probably alter the global environment, in particular by generating stratospheric dust and/or soot loading with ensuing global environmental effects (e.g. Toon *et al.*, 1997). Other alterations, which range from ozone depletion to acid rain, might also affect the global environment (Toon *et al.*, 1997). Such profound disruption of ecological balance might have resulted in dramatic shifts in biological evolution, manifested in the fossil record as extinction boundaries. However, events at such scales are relatively rare. The impact interval is of the order of 10^7 – 10^8 years for impactors that might result in a 10^6 – 10^7 Mt explosion (see Fig. 1). Events that result in only localized alterations to the environment are more frequent. The impact interval is approximately 10^5 years for impactors causing a 10^3 Mt explosion, well within the threshold for regional effects (Toon *et al.*, 1997). These events will result in a localized destruction of the biota such as that proposed for Meteor Crater, Arizona ($35^{\circ} 02' N$, $111^{\circ} 01' W$) (Kring, 1997), a 1.2 km diameter structure formed approximately 5×10^4 years ago. The boundary between global and regional effects is ill defined. At the 23 km-wide Haughton Impact Structure, Devon Island, Canada, ($75^{\circ} 22' N$, $89^{\circ} 41' W$), complete sterilization probably occurred only in the immediate

vicinity of the impact site with material in the impact spall zone being a possible exception.

While the biological and ecological effects of impacts on the global environment are often discussed, the patterns of biological change at the site

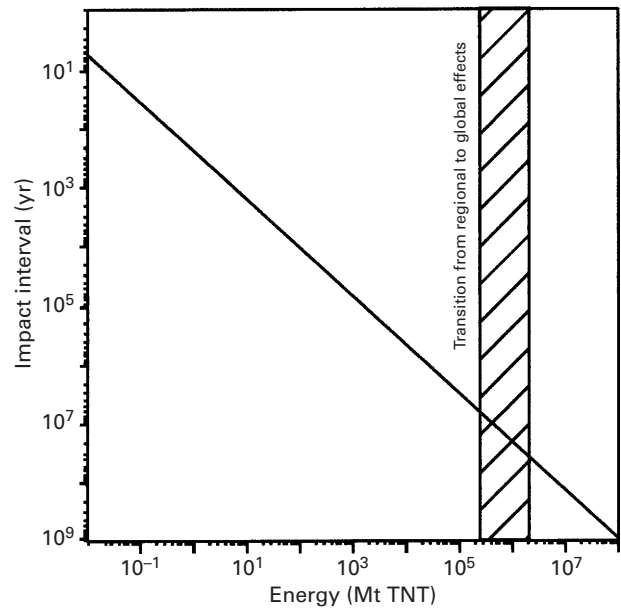


Fig. 1. Time interval between impact events of given energies based on analyses reviewed in Toon *et al.* (1997). The hatched area represents the range of energies associated with the transition between local and global effects. The energy of transition is poorly defined as it depends upon what environmental effect is being considered. The graph illustrates the greater frequency of events that only cause localized destruction. Note that impact energies are often described as equivalent megaton quantities of TNT. 1 Megaton of TNT is equivalent to 4.2×10^{15} J.

Table 1. Asteroid and comet impact craters discussed in this paper listed in alphabetical order

Impact structure name	Location	Diameter (km)	Age (Ma)	Biome
Acraman	Australia (32° 01' S, 135° 27' E)	90	> 450	Chaparral/desert
Amguid	Algeria (26° 05' N, 4° 23' E)	0.45	< 0.1	Desert
Aourunga	Chad (19° 06' N, 19° 15' E)	12.6	< 345	Desert
Avak	Alaska (71° 15' N, 156° 38' W)	12	> 95	Tundra/polar desert
Beaverhead	USA (44° 36' N, 113° 00' W)	60	600	Temperate deciduous forest
Bigach	Kazakhstan (48° 30' N, 82° 00' E)	7	6 ± 3	Temperate deciduous forest
Boltysch	Ukraine (48° 45' N, 32° 10' E)	24	88 ± 3	Grassland
Bosumtwi	Ghana (6° 30' N, 1° 25' W)	10.5	1.03 ± 0.02	Tropical rainforest
Boxhole	Australia (22° 37' S, 135° 12' E)	0.17	0.03 ± 0.0005	Desert
Brent	Ontario, Canada (46° 05' N, 78° 29' W)	3.8	450 ± 30	Temperate deciduous forest
Campo del Cielo	Argentina (27° 38' S, 61° 42' W)	0.05	< 0.004	Grassland
Clearwater (East and West)	Quebec, Canada (56° 5' N, 74° 7' W)	26	290 ± 20	Taiga
Connolly	Australia (23° 32' S, 124° 45' E)	9	< 60	Desert
Crooked Creek	USA (37° 50' N, 91° 23' W)	7	320 ± 80	Temperate deciduous forest
Deep Bay	Saskatchewan, Canada (56° 24' N, 102° 59' W)	13	100 ± 50	Taiga
Des Plaines	USA (42° 03' N, 87° 52' W)	8	< 280	Grassland
El'gygytgyn	Russia (67° 30' N, 172° 05' E)	18	3.5 ± 0.5	Tundra/polar desert
Glover Bluff	USA (43° 58' N, 89° 32' W)	8	< 500	Temperate deciduous forest
Gosses Bluff	Australia (23° 50' S, 132° 19' E)	22	142.5 ± 0.8	Desert
Gow	Saskatchewan, Canada (56° 27' N, 104° 29' W)	5	< 250	Taiga
Haughton	Nunavut, Canada (75° 22' N, 89° 41' W)	24	22.4 ± 1.4	Tundra/polar desert
Haviland	USA (37° 35' N, 99° 10' W)	0.015	< 0.001	Grassland
Henbury	Australia (24° 34' S, 133° 8' E)	0.157	< 0.005	Desert
Holleford	Canada (44° 28' N, 76° 38' W)	2.35	550 ± 100	Temperate deciduous forest
Ilumetsy	Estonia (57° 58' N, 27° 25' E)	0.08	> 0.002	Temperate deciduous forest
Kaali	Estonia (58° 24' N, 22° 40' E)	0.11	0.004 ± 0.001	Temperate deciduous forest

Table 1. (*contd.*).

Impact structure name	Location	Diameter (km)	Age (Ma)	Biome
Kaluga	Russia (54° 30' N, 36° 15' E)	15	380 ± 10	Grassland/temperate deciduous forest
Kelly West	Australia (19° 56' S, 133° 57' E)	10	> 550	Desert
Kentland	USA (40° 45' N, 87° 24' W)	13	< 97	Grassland
Lappajärvi	Finland (63° 12' N, 23° 42' E)	23	77.3 ± 0.4	Taiga
Lonar	India (19° 58' N, 76° 31' E)	1.83	0.052 ± 0.006	Tropical rainforest
Manicouagan	Quebec, Canada (51° 23' N, 68° 42' W)	100	214 ± 1	Taiga
Manson	USA (42° 35' N, 94° 33' W)	35	73.8 ± 0.3	Grassland
Meteor (Barringer)	USA (35° 02' N, 111° 01' W)	1.19	0.049 ± 0.003	Desert
Middlesboro	USA (36° 37' N, 83° 44' W)	6	< 300	Temperate deciduous forest
Montagnais	Nova Scotia, Canada (42° 53' N, 64° 13' W)	45	50.50 ± 0.76	Underwater
Monturaqui	Chile (23° 56' S, 68° 17' W)	0.46	< 1	Mountain zone
Morasko	Poland (52° 29' N, 16° 54' E)	0.1	0.01	Temperate deciduous forest
Morokweng	South Africa (26° 28' S, 23° 32' E)	70	145 ± 0.8	Desert/grassland
New Quebec	Quebec, Canada (61° 17' N, 73° 40' W)	3.44	1.4 ± 0.1	Tundra
Nicholson	Canada (62° 40' N, 102° 41' W)	12.5	< 400	Taiga
Obolon	Ukraine (49° 30' N, 32° 55' E)	15	215 ± 25	Grassland
Odessa	USA (31° 45' N, 102° 29' W)	0.168	< 0.05	Desert/grassland
Ries	Germany (48° 53' N, 10° 37' E)	24	15 ± 1	Temperate deciduous forest
Rio Cuarto	Argentina (32° 52' S, 64° 14' W)	4.5	< 0.1	Grassland
Rochechouart	France (45° 50' N, 0° 45' E)	23	214 ± 8	Temperate deciduous forest
Roter Kamm	Namibia (27° 46' S, 16° 18' E)	2.5	3.7 ± 0.3	Desert
Serra da Cangalha	Brazil (8° 05' S, 46° 52' W)	12	< 300	Tropical rainforest/grassland
Siljan	Sweden (61° 02' N, 14° 52' E)	52	368 ± 1.1	Taiga
Slate	Ontario, Canada (48° 40' N, 87° 00' W)	30	~ 450	Taiga
Steinheim	Germany (48° 41' N, 10° 04' E)	3.8	15 ± 1	Temperate deciduous forest
Sudbury	Canada (46° 36' N, 81° 11' W)	250	1850 ± 3	Taiga

Table 1. (*contd.*).

Impact structure name	Location	Diameter (km)	Age (Ma)	Biome
Tswaing	South Africa (25° 24' S, 28° 04' E)	1.13	0.220 ± 0.052	Grassland
Veevers	Australia (22° 58' S, 125° 22' N)	0.08	< 1	Desert
Vredefort	South Africa (27° 00' S, 27° 30' E)	300	2023 ± 4	Grassland
Wolfe Creek	Australia (19° 10' S, 127° 48' E)	0.875	< 0.3	Desert
Zhamanshin	Kazakhstan (48° 20' N, 60° 58' E)	13.5	0.9 ± 0.1	Mountain zone

Ma, million years ago.

Ages are given with uncertainties (as of August 2001).

of impact craters themselves have received little attention. There are now over 150 identified terrestrial impact craters (R. A. F. Grieve, personal communication) in biomes that range from arctic polar desert to the equatorial forests of Brazil.

Impact craters have for some time been recognized to be sites of unusual ecosystems. Often, the circular or concentric vegetation anomalies have been the initial indication of the presence of an impact structure. In some cases, detailed ecological investigations of impact craters have been undertaken (e.g. Bouchard, 1989; Gronlund *et al.*, 1990; Burba, 1997; Partridge, 1999), but no synthetic study is yet available in the literature. Although impact craters are found in many biomes and regions of the world, they share some basic ecological characteristics that are driven by their specific mechanisms of formation and their physical characteristics. Overlain on these general similarities are the effects of the specific climatic regimes and biomes in which the crater happens to have formed and resides, providing interesting insights into how the ecology of specific impact craters can be influenced by their location.

All catastrophic events that can cause the formation of primary succession habitats (habitats that are completely bare for recolonization); for example high intensity fires, volcanism, and also glacial scouring, have their own unique patterns of recovery. The concepts of succession that occur after these events are directly applicable to ecological recovery at the site of asteroid and comet impacts (Cockell *et al.*, 2001*b*). Because of the significant differences between impact events and other mechanisms that cause local ecological disturbance, the patterns of biological recovery and change at the site of impact craters merit separate analysis. Here, we review

some of the biological and ecological characteristics of impact craters and we propose a generalized sequence of post-impact succession.

II. IDENTIFYING COMMON PATTERNS IN POST-IMPACT BIOLOGICAL CHANGES

(1) Existing studies

Knowledge of the patterns of biological recovery at the site of impact events is still sparse. In order to begin to understand the trends that occur, we first undertook a review of the existing literature. The craters discussed are shown in Table 1. Previous studies of the present-day biota of the New Quebec impact crater-lake, Canada (61° 17' N, 73° 40' W) guided us in considering the biology of impact lakes (Gronlund *et al.*, 1990), which we supplemented with the data of Maltais and Vincent (1997) on the Clearwater crater-lakes, Canada (56° 5' N, 74° 7' W) and the data of Ashton (1999 and references therein) on the lake of the Tswaing impact crater, South Africa (25° 24' S, 28° 04' E). We also supplemented our discussions with the considerable data that exist on volcanic lakes. On land, the work of Burba (1997) on the present-day ecology of four impact structures, together with the work of Kring (1997) on the present-day biology of Meteor Crater, USA (35° 02' N, 111° 01' W) guided us in considering possible successional patterns in the terrestrial realm and the characteristics of present-day impact crater biology.

(2) The Houghton impact structure

We considered the above work in the context of our on-going biological studies at the Houghton impact

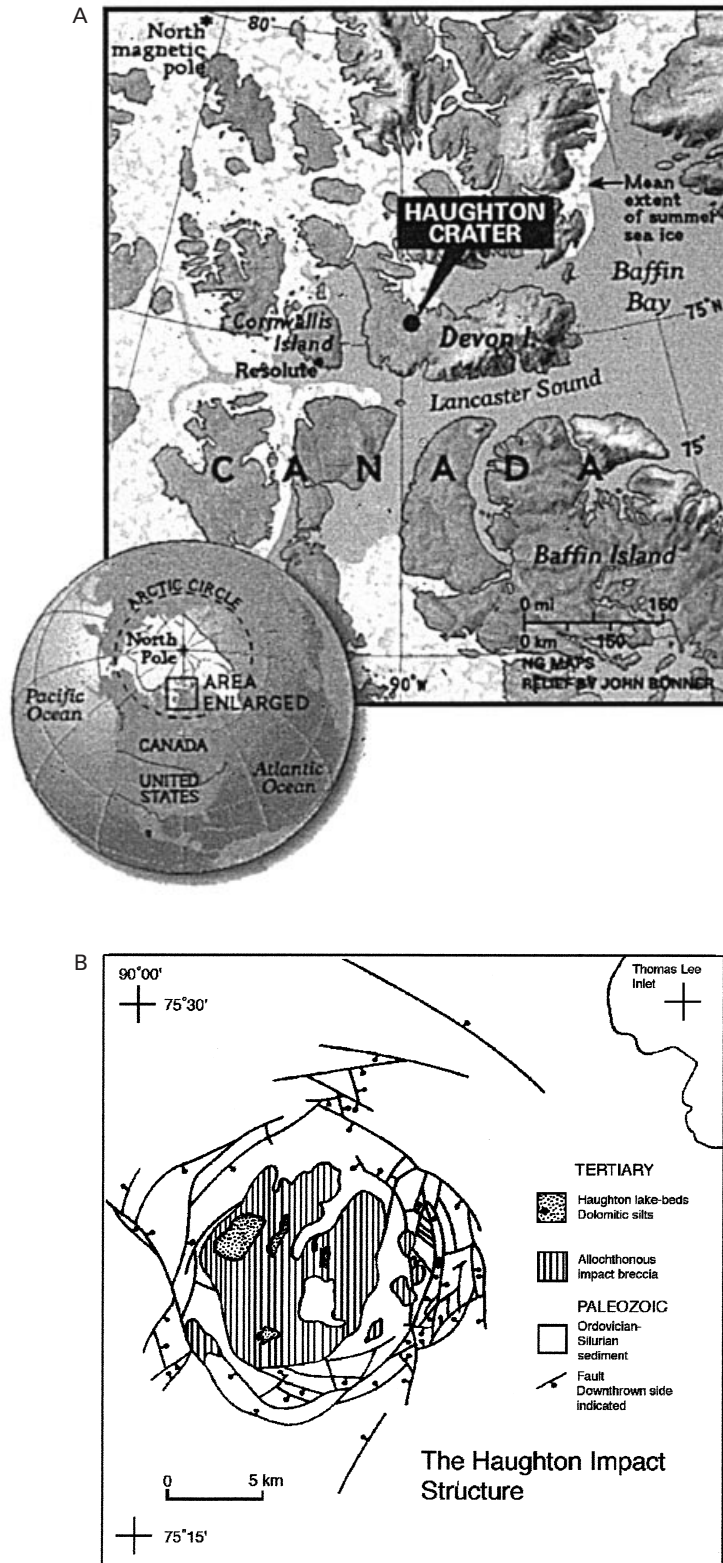


Fig. 2. (A) Map of the arctic showing the location of the Haughton impact structure, Devon Island, Nunavut Canada (modified from Long, 1999). (B) Map of impact faults and major geologic units of the Haughton crater (adapted from Hickey *et al.*, 1988).



Fig. 3. Synthetic Aperture Radar image of the Haughton impact structure, Nunavut, Canada (Canadian Geological Survey).

structure, Devon Island, Canada during the 1997–2000 summer field seasons.

The Haughton impact structure is situated on Devon Island in the Canadian Arctic Archipelago (Figs 2 and 3). It was formed 22.4 ± 1.4 million years ago (Ma) in the early Miocene (Omar *et al.*, 1987). Its impact origin was proposed by Dence (1972) from airphoto and cartographic interpretation, and confirmed by Robertson and Mason (1975) on the basis of field observations. Subsequent studies made under the auspices of the Haughton Impact Structure Study (HISS) Project provided more detailed characterization of the structure (Grieve, 1988 and references therein). The gravity low associated with fractured impact rocks defines the diameter of the structure as 24 km (Todd, 1978; Pohl, Eckstaller and Roberston, 1988).

The Haughton crater was formed in target rocks dominated by a subhorizontal sequence of Paleozoic sedimentary rocks, mostly carbonates, underlain by a basement of Precambrian granites and gneisses.

The formation of the crater was accompanied by the emplacement of an allochthonous impact breccia unit, which can still be found at the site in a well-preserved state (Grieve, 1988; Redeker and Stoffer, 1988). The breccia is a polymict assemblage of target rock clasts, hence composed predominantly of carbonates. Following impact, the breccia unit covered most of the crater floor.

The biological characteristics of the Haughton impact structure are rather unique among known impact structures because of its exceptional high arctic setting. This setting has promoted the good preservation of distinctive geologic features such as the allochthonous breccia unit and paleosediments from a post-impact lake, formations that are often quickly eroded or buried at other impact sites because of their inherent erodibility and/or location in topographic lows. Moreover, the relatively low biological diversity, and the low rates of high arctic plant growth, characteristic of polar desert environments (Chapin, 1980) make Haughton particularly

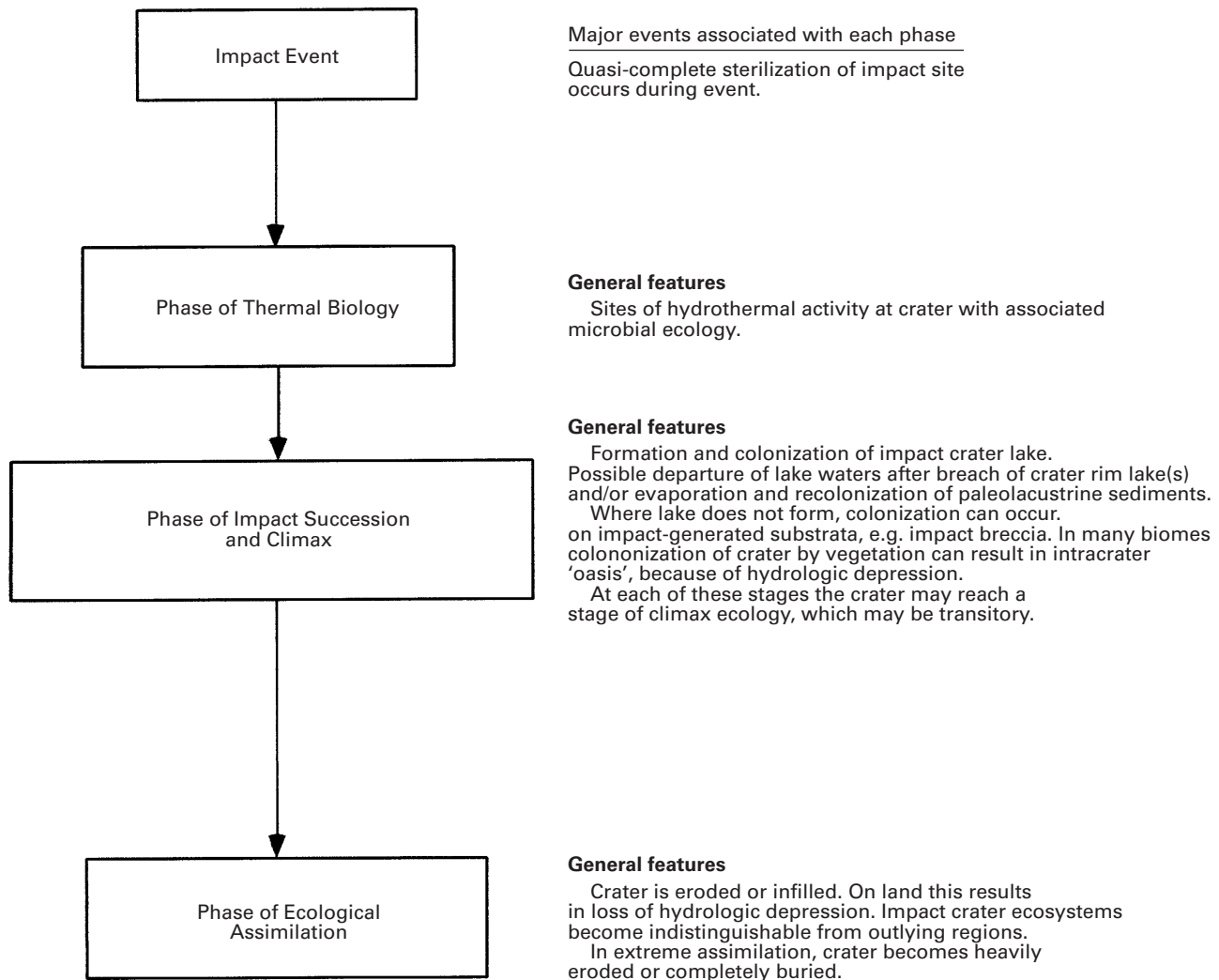


Fig. 4. The major phases of post-impact recovery at the site of impact craters that are distinguished in this review. Details are described in the text.

useful as a simplified biological system for studying impact crater recolonization.

There are a number of other reasons for the interest in Haughton. Firstly, as well as allowing its present-day biology to be examined in an analogous way to other biological studies of impact structures (Bouchard, 1989; Gronlund *et al.*, 1990; Burba, 1997), the good paleobiological record preserved at Haughton has provided unique insights into the past biological characteristics of the crater's region (Frisch and Thorsteinsson, 1978; Roberston and Sweeney 1983; Roberston *et al.*, 1986; Hickey, Johnson and Dawson, 1988). Secondly, the unusual ecology of impact craters has been characterized in both the aquatic realm (e.g. Bouchard, 1989; Gronlund *et al.*, 1990) and the terrestrial realm (Burba, 1997). Haughton combines both. Like some other impact craters, Haughton was once dominated

by aquatic succession during the period in which it possessed impact lake(s). It is now an impact ecosystem dominated by land processes. Thirdly, the previous geological characterization of the crater (Grieve, 1988; Robertson and Sweeney, 1983, and references therein) together with the on-going geological work under the auspices of the NASA Haughton–Mars Project (Lee *et al.*, 1998) allowed us to develop a perspective on the potential biological attributes of craters after impact that underscores their exobiological significance.

The observations have some obvious limitations. The biota we observe in Haughton today is post-Miocene, post-glacial (in common with some other Canadian impact structures such as New Quebec that were glaciated before the end of the Last Glacial Maximum approximately 8000–10000 years ago), not merely post-impact. However, comparisons

between the biota on impact-processed substrata such as the breccia and on non-impact substrata such as the alluvial and fluvio-glacial terraces of the Houghton River, allow us to comment on potential generalized mechanisms for the recolonization of an impact substratum (Cockell *et al.*, 2001*b*) that can be compared with successional mechanisms following other types of ecological disturbance.

In addition to our observations at Houghton, we supplemented this study with direct biological observations that we have made at other impact craters, including the Tswaing impact crater, South Africa (Cockell *et al.* 2001*a*), and also Barringer Crater (Meteor Crater), Arizona; the Beaverhead impact structure, Montana; Brent Crater, Ontario; the Henbury craters, Australia; Monturaqui Crater, Chile; Odessa Crater, Texas; the Sudbury impact structure, Ontario, and the Vredefort impact structure, South Africa.

Necessarily, some of the discussion presented in this review is based on inference and deduction from other, similar, ecological agents of disturbance. In the absence of a very recent impact crater (< 100 years) that would allow for successional and ecological studies from a time point immediately following impact, the biological attributes of existing impact craters must be used as judiciously as possible. The Tunguska impact event of 1908 in Siberia, Russia (approximate epicentre 61° N, 102° E) potentially offers some insights into post-impact ecological processes, particularly secondary succession after the airburst-induced destruction of the forest in this case, but the lack of a crater makes it of less interest from the point of view of our focus here.

In the present review, we distinguish three phases, which we term the Phase of Thermal Biology, the Phase of Impact Succession and Climax, and the Phase of Ecological Assimilation (Fig. 4). We use these three general divisions to order the discussion in this review, but more importantly because they emerge as representing three key distinct stages in the patterns of post-impact biology and ecologic recovery at impact sites.

III. THE CHRONOLOGICAL SEQUENCE OF POST-IMPACT ECOLOGY

(1) Phase of Thermal Biology

(a) Physical constraints

At the site of a large impact event, pressures and temperatures of the order of several hundred GPa

and 15000 K are achieved, leading to rock vaporization in both the impactor and the target (Melosh, 1989). Once formed, the crater presents a regional thermal anomaly resulting from two effects: (1) conversion of part of the projectile's kinetic energy into heat, and (2) the upward mobilization of hot target material from depth, which in the case of larger craters and considering a normal initial geothermal gradient, may result in a significant source of additional heat at the impact site. However, any heat made available from these two effects will be transient, as the warmed target rocks will eventually cool in the absence of a sustained source of heat. Cooling will occur mainly by conduction through subsurface rock, radiation at free rock surfaces, and convection through contacting water and air (Melosh, 1989). Groundwater circulation, while being presented with a local opportunity for hydrothermal cycling, will promote faster cooling overall.

The phase of thermal biology may be defined as that during which the thermal anomaly associated with a recently-formed impact crater sustains biological activity of a nature or at a level requiring warmer environmental conditions than would be available in the same area had the impact event not occurred.

The duration of the phase of thermal biology is difficult to estimate in any detail, but will generally be extremely short compared to the normal geologic lifetime of an impact structure. In the case of a 24 km-diameter crater such as Houghton, assuming simple conductive cooling and no groundwater circulation, thermal readjustment of the bulk of the crater basement to a mean temperature of < 50 °C is estimated to be achieved after several thousand years (Osinski, Spray and Lee, 2001). Similar time periods were estimated for the cooling of the 200 m suevite layer in the Ries impact crater, Germany (Pohl *et al.*, 1977). Because of the ubiquitous presence of groundwater on Earth, convective cooling usually plays an important role as well, resulting in the formation of impact-induced sites of hydrothermal activity. Degassing pipes and clay alteration phases have been found at the 27 km-diameter Ries crater, Germany that attest clearly to hydrothermal activity (Newsom *et al.*, 1986). At the Ries, temperatures in excess of 500 °C presided over the formation of the degassing pipes in the suevite deposits, while hydrothermal alteration of these deposits occurred at or below 100–130 °C (Newsom *et al.*, 1986). Hydrothermal signatures can also be found at relatively small craters. Such signatures have been identified at

the 2.5 km-diameter Roter Kamm crater, Namibia (27° 46' S, 16° 18' E) where hydrothermally altered melt breccias have been reported (Koeberl *et al.*, 1989). In the case of the Boltysh impact crater in the Ukraine, hydrothermal heating appears to have continued well after the formation of the crater-lake, since the heated water may have caused secondary alteration of minerals through silicate dissolution and other processes. Eventually, when the water cooled, precipitation of minerals such as clinoptilolite occurred (Gurov, 1996). In general, the magnitude and duration of any phase of thermal biology at an impact crater will scale with the dimensions of the structure: the more energetic the impact, the more heat delivered and the longer the duration of any thermal phase. No impact crater on Earth at present is experiencing its initial phase of thermal biology.

The issue of impact-induced volcanism, which is often considered in discussions of larger structures such as Sudbury and Vredefort and could also represent an opportunity for impact-induced thermal biology, remains controversial (Melosh, 1989). The controversy lies in the question of whether the volcanic activity is triggered by the impact event itself or whether it would occur anyway and is merely locally "hosted" by the impact structure. In the case of the Moon for instance, impact basins have served as topographic depressions with fractured basements, which were used as hosts and partially filled by magmatic outflows resulting from volcanic activity that took place long after the basins themselves formed.

While in some instances comparisons between impacts and volcanism are useful, there are significant differences. With respect to ecology, impacts and volcanism present three main differences: (1) after the heavy bombardment phase early in Earth's history, impacts on our planet have been mostly isolated events of extremely limited duration. On geological timescales, impacts represent short pulses of delivered energy. Volcanism by contrast, is often characterized by energy release sustained over long periods of time, particularly in the case of continental-scale events (Rampino, Self and Stothers, 1988), albeit often through a succession of pulses (eruptions). (2) The geologic disruption induced by impacts is typically more localized than that associated with volcanism. While impacts may affect the terrestrial environment on global scales, the volume of material actually subjected to significant heating, shock, disruption, and ejection is generally limited to the crater and ejecta blanket. Volcanism,

by contrast can result in substantial volumes of material experiencing heating. Some large-scale volcanic events can result in the formation of basalt flood plains that extend over many thousands of square kilometers, such as the Indian Deccan traps that cover approximately 0.5 million square kilometers (Subbarao, 1999). (3) Materials affected and processed by impacts can be of any nature, as impacts are fundamentally an exogenous process. Volcanism in contrast, will produce materials that are significantly more homogenous and uniform in composition: by definition, volcanic rocks and volcanically altered materials. Impacts into targets composed of volcanic rocks present a situation where the biological effects of the two processes may be compared with one fewer variable. The Lonar crater, India, (19° 58' N, 76° 31' E), was formed in Deccan traps basalts (Fredriksson *et al.*, 1973) and offers a rare opportunity to explore issues of biological contrast between the effects of volcanism strictly and impacts. Table 2 discusses some of the differences and similarities between impact events and volcanism.

(b) *Hydrothermal biology*

Can biological activity be sustained at an impact site during this initial thermal phase, and what might the nature of this activity be? There are at present no published data presenting clear evidence for life at an impact site associated strictly with the so-called Phase of Thermal Biology. There is, however, reasonable basis for hypothesizing such life. The establishment of a transient hydrothermal system at a freshly formed crater might provide a temporary habitat for associated microbiological communities. Provided the duration of the thermal phase is sufficient, such a habitat could host thermophilic communities (optimum temperature growth ≈ 80 °C) similar to those observed in volcanic and other geothermal hot springs (Segerer *et al.*, 1993) with their associated diversity (Barnes *et al.*, 1994). The existence of thermophilic organisms on early Earth has been suggested to be correlated with their ability to survive impact events (Sleep *et al.*, 1989). Thermophilic organisms are metabolically versatile and as well as being able to use the various oxidation states of sulphur, they can make use of ferric iron and other substrates as alternative energy sources (Segerer *et al.*, 1993; Schonheit and Schafer 1995). Ecosystems of thermophilic organisms might prosper at freshly-formed impact craters, perhaps similarly to the hydrothermal volcanic vents on the summit of

Table 2. *Some geological features of impact craters and the consequences for their biological characteristics. A comparison is made with volcanism to illustrate the similarities between some aspects of these events*

Physical feature of impact event	Biological consequence	Associated with sites of volcanic activity?
Sites of impact-induced hydrothermal activity	Provides habitats for thermophilic, mesophilic, psychrophilic or -trophic organisms depending on duration of hydrothermal activity and latitude of impact	Yes
Crater rim/crater islands	Endemism of enclosed biota. Known for impact lakes (e.g. New Quebec). Not demonstrated for terrestrial habitats (such as isolation of organisms within impact uplift ring)	Yes, in some volcanic crater lakes
Crater lake	Succession in lacustrine environment. Possible isolation of enclosed biota	Yes
Paleolacustrine deposits	Paleolacustrine deposits from ancient crater lake can provide biologically enriched areas in otherwise depauperate regions, for example in polar regions (e.g., Haughton)	Can occur if crater lake breaches
Impact-generated substratum	Results in large areas of impact basin covered by oligotrophic impact-generated substrata, which may be different in its mineralogical and pH characteristics compared to non-impact substrata (may also include extraterrestrial input of materials)	Can occur with volcanic breccia, but no pressure effect during breccia formation and not necessarily localized within area of crater
Rocks modified by impact metamorphism	Provides habitats for chasmolithic and sublithic organisms and possibly endoliths in some substrates. Water flow in rocks allows for enhanced biological productivity (see 'sites of impact-induced hydrothermal activity')	Not as extensively as impact craters
Basin deeper than surrounding land (impact-induced oasis)	May provide advantages in drainage for plants and microbial communities in crater. In some cases may be a disadvantage to biological communities inside crater if salt deposits or sands collect	Yes

Loihi Seamount, Hawaii, in which iron-oxidizing bacteria are a major constituent (Karl, Brittain and Tilbrook, 1989).

How might the hypothesized post-impact thermal biology leave a trace? It is already apparent that ancient thermal spring deposits leave a record of microbial communities in the form of stromatolites, microfossils, isotope patterns and remnant biomarkers (Walter, 1996). Photosynthetic organisms are known to be able to leave paleobiological signatures at the site of impact craters. Microbial tufa deposits built by the green alga *Cladophorites* are embedded in the carbonate facies of the Ries crater. The tufa deposits were built when the basin was filled with a crater-lake approximately 14 Ma ago (Riding, 1979). Although they are not associated with the phase of thermal biology, but rather a later phase of recolonization, they provide an excellent example of biomineralization at the site of impact craters resulting from organisms specific to the impact site. Warm water outflows at the surface of a crater would allow aerobic phototrophic communities to develop with their associated consortia of organisms as is seen in other hydrothermal settings such as volcanic crater-lakes (Dymond, Collier and Watwood, 1989) and geothermal environments (Nold and Ward, 1995) where cyanobacterial mats often grow in the outflows of water vents.

In the case of pelagic impacts, underwater hydrothermal venting might favour the localized growth of some genera of organisms similar to those associated with sub-sea hydrothermal vents (Prieur, Erauso and Jeanthon, 1995).

Finally, the phase of thermal biology, through its microbial activity and water availability, could support higher trophic levels such as plants, invertebrates and vertebrates that become associated with the enhanced primary productivity of the site.

(c) Planetary and exobiological significance

In spite of the current lack of definitive data, the phase of thermal biology is of tantalizing interest with respect to planetary sciences and exobiology as impacts represent a significant source of heat in cold extraterrestrial environments, if only locally and transiently (Newsom *et al.*, 1996).

Impact craters on Mars may have experienced interactions with liquid water, either from impact-induced melting of near-surface ice and/or because the craters formed in epochs when liquid water was more readily available on Mars (e.g. Cabrol and Grin, 1995). The possibility of the prolonged

existence of liquid water on Mars is a subject of particular exobiological interest (e.g. McKay and Davis, 1991). Newsom *et al.* (1996) investigated the survival time of impact crater-lakes on Mars with water being contributed by penetrated aquifers and the associated gradual thickening of an ice cover. They concluded that large impact craters on Mars (> 65 km in diameter) could have sustained ice covered lakes for approximately 10^3 – 10^4 years.

No terrestrial impact craters have yet been established to have formed in ground-ice-rich target rocks. The El'gygytgyn crater, Russia (67° 30' N, 172° 05' E), might be a case where such a circumstance occurred. The crater is presently located in the zone of continuous permafrost in north-eastern Siberia and formed only 3.5 million years ago, in late Cenozoic times, when permafrost was probably present at the site. This is not the case for Haughton, which formed in the early Miocene, i.e. during a period of more clement conditions in the High Arctic prior to Tertiary cooling. The target rocks at Haughton were probably not underlain by significant permafrost at the time of impact (Leo Hickey, personal communication). Relict permafrost at greater depth also appears unlikely, as the Oligocene, which preceded the Miocene, was globally warmer still.

In the case of Saturn's moon Titan, impacts could result in transient melt pools of liquid H₂O (or H₂O + NH₃) in which aqueous organic chemistry could take place (Thompson and Sagan, 1992). Craters approximately 10 km in diameter have been estimated to be able to maintain such melt pools for approximately 10^3 years (Thompson and Sagan, 1992). In the absence of any significant source of internal heating, such impacts might provide unique opportunities for prebiotic chemical complexification on Titan. It has been suggested that on early Earth cometary impacts may have led to organic enrichment, either by direct input or by shock synthesis (Clarke 1988; Chyba *et al.*, 1990).

Europa is another case where impacts could result in transient melt pools in which aqueous organic chemistry could take place. However, internal heating of tidal origin is a dominant resurfacing process on this jovian satellite, possibly sustaining a present subsurface ocean (Reynolds, McKay and Kasting 1987). The contribution of impacts to any prebiotic chemistry on Europa would likely be secondary.

Thus, in cold extraterrestrial environments such as the surfaces of Mars, Europa or Titan, impacts may offer, through their ephemeral thermal phase,

episodic opportunities for enhanced chemical activity of relevance to biology.

Note: impacts into gaseous planets may be important as well from the standpoint of affording opportunities for the synthesis of chemical compounds of significance to prebiotic chemistry and possibly biology, but as no impact crater is formed in this case, the topic lies outside the scope of the present review.

(2) Phase of Impact Succession and Climax

Impact events offer remarkable examples of allogenic succession, i.e. succession in which factors other than the biota direct the course of successional change. Once the area of the impact has begun to cool, a process of invasion or recolonization by the outlying biota can occur that depends in large part upon the geological characteristics of the impact crater. The gross nature of this process will firstly depend upon whether a crater-lake forms within the impact basin. If the crater rim is partially breached, the formation of an impact crater-lake may be impeded. In the case of the Haughton crater, a lake (Hickey *et al.*, 1988) or possibly several small lakes formed almost immediately after impact. The lake will not only have important ecological implications for the direction of succession in the aftermath of the phase of thermal biology, but as will be discussed, the lacustrine deposits may continue to influence ecological development for a considerable time after the departure of lake waters.

(a) *The impact crater-lake*

(i) *Impact crater-lake arrangements*

Intracater-lakes can present simple to complex configurations depending on the crater's topography and the local abundance of water. The New Quebec crater, Canada, offers an example of a simple crater lake whereas the Brent crater, Ontario, Canada (46° 05' N, 78° 29' W), with its two large water bodies separated by a raised ridge within its perimeter, is an example of a more complex configuration. Intracater lakes can also be connected to outside water bodies in places where the impact crater lies near rivers or in coastal regions. Thus, distinctive mixed water/land topographies arise, as seen in a number of impact craters. Some excellent examples are found in Canada (Robertson and Grieve, 1975), including the Clearwater West crater, Quebec, which is now an impact lake containing an internal island ring surrounding the

water-filled centre of the structure; Gow crater, Saskatchewan, (56° 27' N, 104° 29' W), which has a central uplift region surrounded by a lake which connects to outlying lake bodies; and Manicouagan, Quebec (51° 23' N, 68° 42' W), a 100 km diameter impact structure, which has a circumferential water moat connected to outlying water sources (Fig. 5). In the case of Manicouagan, however, this configuration is largely due to hydroelectric damming. The Slate Islands, Ontario, Canada, (48° 40' N, 87° 00' W), correspond to the central uplift of an impact structure now submerged under the northern portion of Lake Superior. In some cases, a cluster of lakes can result from multiple impacts. Six of the eight Morasko craters, Poland (52° 29' N, 16° 54' E), are small shallow lakes found in beech forest (Classen, 1978).

Depending upon the location of the crater and the climatic regimen, some of these lakes are seasonal and only prevalent during periods of precipitation such as the Acraman crater-lake, Australia (32° 01' S, 135° 27' E). The floors of this structure are occupied by high-albedo saline playas (Williams, 1994). Highly saline but perennial bodies of water result where evaporation is less extreme, as in the case of the briny lake at Lonar crater, India, which is located under a subtropical climate (Fredriksson *et al.*, 1973). Conversely, the water table may be currently low enough that water ponding is not experienced at present although it was in the past. Barringer Crater (Meteor Crater), Arizona, and Wolfe Creek Crater, Australia, are examples of such situations.

(ii) *Microbial profiles of impact crater-lakes*

In crater-lakes, recolonization and succession will occur as microorganisms are transported in from outlying regions. Studies on the microbiology of the 267 m-deep lake at New Quebec crater, Canada (Fig. 5B), a 3.4 km wide crater (1.4 Ma) show that many of the species are wind-borne, originating from outside the crater rim (Gronlund *et al.*, 1990). The process of post-impact limnological colonization could potentially be quite rapid. Colonization of newly formed water bodies in the blast zone of the Mount St. Helens volcano, Oregon, some associated with warm benthic springs, occurred within three to four months after the eruption in 1980 (Ward *et al.*, 1983). This is similar to the role proposed for the hydrothermal-upwelling-induced growth of microorganisms in the volcanic Crater-lake, Oregon (Dymond *et al.*, 1989). Thus, in these situations,

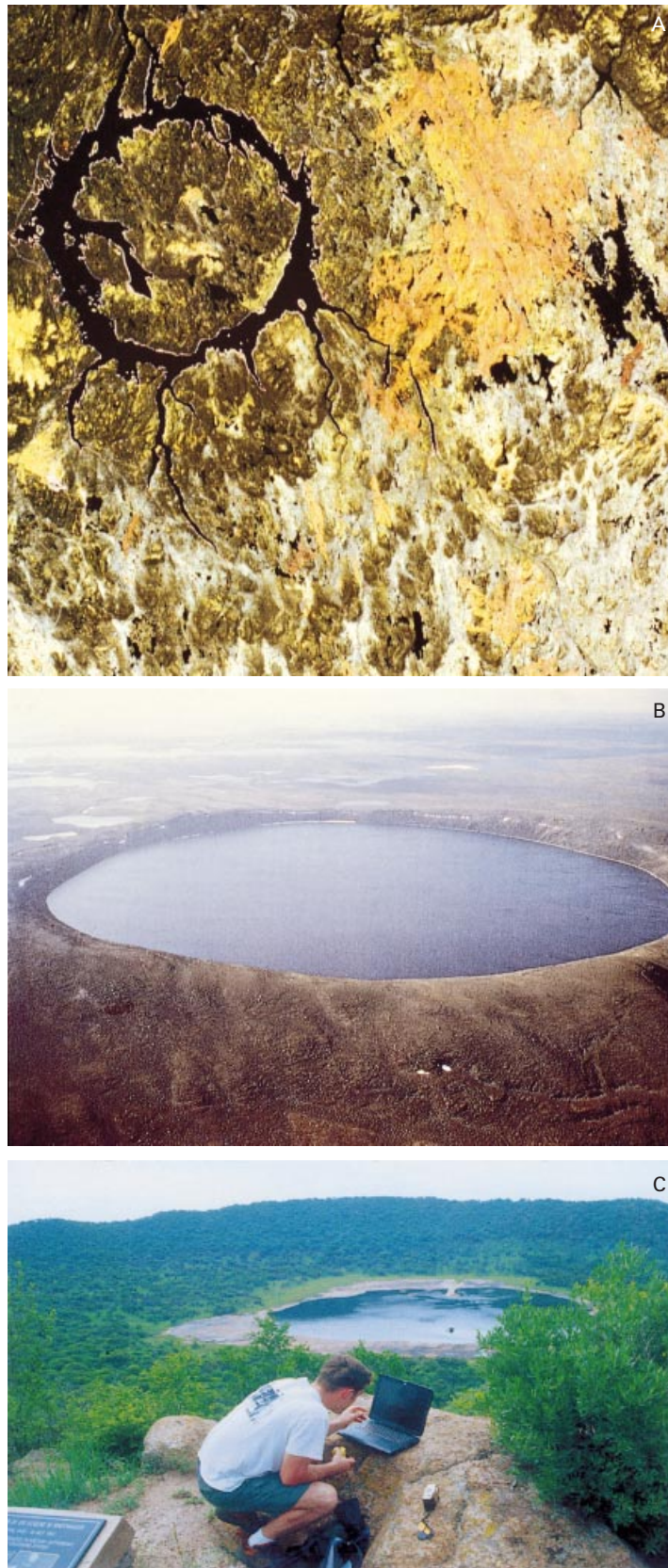


Fig. 5. Three lake-filled impact craters. Manicouagan (A) is 100 km in diameter. The annular ring was caused by the erosion of impact-brecciated rock during the last glaciation. The formation of a lake in the ring is caused by damming, illustrating an involvement of human activity in the characteristics of impact craters (photo, NASA). New

recolonization of the lake may partly be a function of the phase of thermal biology since the proliferation of the recolonizing microbial communities could be enhanced by impact-induced heat lingering from the impact event.

A limitation in examining modern day lakes is that their biota may not reflect the biota that immediately invaded the lake after the impact event. However, the modern day lakes may still bear some of the key characteristics of the original lake(s), many of which are directly the result of a crater's structure itself, and can give instructive insights into some of the ecological attributes of the lakes throughout their successional history. For example, impact crater lakes are often characterized by steep sidewalls, e.g. the Deep Bay impact structure, Saskatchewan, Canada (56° 24' N, 102° 59' W) and the New Quebec crater (sides are 25–35°), relative to lakes formed by other processes. In these impact crater-lakes, the littoral zone is of very limited extent, resulting in a relatively oligotrophic (nutrient-poor) water body (Gronlund *et al.*, 1990). In the New Quebec crater-lake, epiphytic diatoms are of low abundance because of the limited littoral zone (Gronlund *et al.*, 1990). By contrast, the Clearwater lakes were found to have rich periphyton diversity, dominated by cyanobacteria such as *Gloeocapsa* and *Calothrix* spp. (Maltais and Vincent, 1997). These lakes are less deep than New Quebec (maximum depth of the Eastern Clearwater lake was 178 m and the mean depth is 60 m compared to the 267 m maximum depth of New Quebec), but they cover a much greater area (approximately 30 km diameter for the Eastern lake compared to 3.4 km diameter for New Quebec) and have irregular channels and islands along their edges, perhaps creating greater opportunity for littoral zone organisms compared to the more morphologically regular New Quebec crater.

A comparison between the biota of two impact crater-lakes can help us understand the importance of local geological, biological and climatic conditions on determining the characteristics of their lakes. Two well-characterized lakes are the New Quebec and Tswaing impact crater-lakes (Delisle, Bouchard and Andre, 1986; Gronlund *et al.*, 1990; Ashton and Schoeman, 1988; Schoeman and Ashton, 1982). The New Quebec crater-lake is almost perfectly

circular and holds a volume of 0.9 km³. The diameter of the structure is 3.4 km. The lake waters are clear (1% of incident light reaches 87 m) and temperatures are relatively constant at approximately 2.5–3 °C down to the bottom (267 m) of the lake. The mean depth is 200 m. The cold arctic conditions, short growing season and the slightly acidic lake water (pH approximately 6.0), together with the impact-basin-induced oligotrophy has resulted in a biota specific to the lake that is dominated by acidophilous and arctic species of diatoms such as *Eunotia arctica*, *Cyclotella stelligera* and *Tabellaria flocculosa* and the arcellacean *Diffugia oblonga*. There are also various morphologically anomalous forms of diatoms. This is attributed to the harsh physical conditions and oligotrophy associated with the lake. Many of the diatoms are smaller than European counterparts. The zooplankton diversity is also very low (Delisle *et al.*, 1986). Only briefly in early post-glacial times did the lake establish contact with neighbouring lakes (Bouchard and Saarnisto, 1989), which may account for the presence of the lake's arctic char population. Using samples recovered from the bottom of the New Quebec crater, Gronlund *et al.* (1990) showed that the chemical profile of the lake waters has remained similar for approximately 5000 years.

By contrast the Tswaing impact crater has a very different microbiology. Set in the South African bushveld (Fig. 5C), the 1.13 km diameter structure is filled with vegetation, primarily *Acacia* and *Combretum* spp. The area is characterized by erratic rainfall (between 400–750 mm a year) and summer temperatures that vary between a mean minimum and maximum of 14.2 °C and 35.2 °C, respectively. In the center of the crater is a saline lake with a mean depth of 0.49 m and a maximum depth of 2.85 m at high water level. Na⁺ concentrations range from 29 g l⁻¹ to 103 g l⁻¹ from the surface to the bottom of the lake. In the summer, the midday surface temperature of the lake can rise as high as 33.8 °C, and still up to 19.7 °C in winter. The planktonic algae and bacteria (primarily *Spirulina* and *Anabaena* spp. and *Halobacter* spp. respectively) inhabit the surface water and productivity is high (2.0–5.0 gCm⁻² day⁻¹). A plate of photosynthetic sulphur bacteria occupies a zone below the zone of maximum temperature. Light transmission is reduced to prac-

Quebec impact lake (B), a 3.3 km impact lake. The poor littoral zone, caused by the steep sides of the impact crater, is evident in the image. It contributes towards the oligotrophic nature of the lake. Tswaing impact crater (C) is a 1.1 km diameter impact structure situated in South African bushveld containing a hypersaline lake in its centre (photograph, Charles Cockell).

tically zero at a depth of 40 cm. The Secchi disk depth in the summer was 7 cm (a Secchi disk is a 20 cm disk with alternating black and white quadrants. It is lowered into the water of a lake until the observer can no longer see it. This depth of disappearance, called the Secchi depth, is a measure of the transparency of the water). This depth can be compared to 1% transmittance at 87 m in the New Quebec structure. The low Secchi disk depth in the Tswaing impact crater is because of the rich phytoplankton populations and the humic substances that leach into the lake from the crater vegetation.

The large diversity in the microbiology of impact lakes that is inferred from the limited knowledge of the few that have been studied is expected. Volcanic crater-lakes show huge global diversity in their microbiota, which may be determined, among other parameters, by salinity, temperature, dissolved oxygen concentrations, and dissolved inorganic and organic carbon (e.g. Green, Moghraby and Ali, 1979; Southern *et al.*, 1986; Banderas Tarabay, Gonzalez Villela and De la Lauza Espino, 1991; Kizito *et al.*, 1993).

Furthermore, it is important to note that these microbial systems are by no means constant over time. The Bosumtwi impact crater-lake in Ghana (6° 30' N, 1° 25' W) is characterized by an anoxic bottom layer and a more oxygenated biologically richer top layer (Turner *et al.*, 1996). However, the geochemistry was observed to have altered over a relatively short period of time (decades) due to changes in lake levels (Turner *et al.*, 1996). Similar variations in lake salinity over time have been proposed from evidence in the paleolacustrine deposits at the Ries impact crater, Germany (Dehm *et al.*, 1977). Thus, changes in the lakes themselves may drive changes in the biota over time. In cases where more than one unconnected lake forms, it is possible that the impact basin may play host to quite different biotas, depending upon local chemistry.

(iii) *Impact crater-lakes and the significance of their paleobiological record*

Impact crater-lakes are sites of great scientific value as they may provide otherwise unavailable depositional environments in which the flora and fauna from surrounding biomes are collected and become preserved. Indeed, there are cases where intracrater paleolacustrine sediments provide a unique record of a region's paleobiology.

At Haughton for instance, after impact a crater-

lake, or possibly several crater-lakes, formed that rapidly led to the deposition of sediments on top of the breccia (Frisch and Thorsteinsson, 1978; Roberston and Sweeney, 1983; Roberston *et al.*, 1986; Hickey *et al.*, 1988). The biostratigraphical record within these paleolacustrine sediments (the Haughton Formation) has provided valuable insights into the ecology of the region at the time immediately following impact (Hickey *et al.*, 1988; Whitlock and Dawson, 1990). They are unique because no other formations have been identified that reveal the ecology of the early Miocene in the High Arctic prior to the onset of Tertiary cooling in the Pliocene (Hickey *et al.*, 1988). At the time of impact, the region in which the crater formed had a mean annual temperature of between 8 and 12 °C and a growing season of between 120 and 200 days. Palynomorphs (pollen samples) have provided correlated climatic and ecological data attesting that at the time of impact, the timberline was as far north as Devon Island (Hickey *et al.*, 1988; Whitlock and Dawson, 1990). The flora of the Haughton Formation suggests that the ecological setting at the time was equivalent to the present-day mixed conifer/northern hardwood forests that lie between the southern deciduous forests and the more northern circumboreal forests (Hickey *et al.*, 1988; Whitlock and Dawson, 1990). Although the climate was more clement than at present, it was still a low arctic climate. The evidence is supported by fossil fish remains from the Haughton Formation that are species of trout (*Eosalmo* spp.) and smelt-like fish (cf. *Osmerus* spp.), which are characteristically cool water fishes (Whitlock and Dawson, 1990). Included in the paleolacustrine deposits at Haughton are early Miocene rabbits, rhinoceroids, fish, shrews and other highly endemic and derived faunal remains (Hickey *et al.*, 1988; Whitlock and Dawson, 1990). These records therefore provide insights into the ecological characteristics during the initial succession period.

Following possibly a breach in the rim of Haughton crater, the post-impact lake waters drained, and since that time much of the original lacustrine sediments have been subject to erosion, leaving at present only a patchy distribution of sedimentary veneers. The largest and thickest remaining outcrop of the Haughton Formation covers approximately 7 km² and lies in the north-western portion of the crater, between the Rhinoceros and Cataclastic creeks (Hickey *et al.*, 1988).

In the New Quebec crater-lake, the bottom sediments have escaped glacial erosion during the Cenozoic glaciations and thus hold a unique bio-

stratigraphical record associated with the glacial and interglacial cycles of the Cenozoic (Gronlund *et al.*, 1990).

Other examples of craters with examined paleo-lake deposits, some of which are submerged at present, include the Ries crater, Germany (Pohl *et al.*, 1977; Hoeffling *et al.*, 1977; Dehm *et al.*, 1977), the Brent crater, Canada (Lozej and Beals, 1975), the Lake Kaali structure, Estonia (58° 24' N, 22° 40' E) (Saarse *et al.*, 1991), the Lappajärvi impact structure, Finland (63° 12' N, 23° 42' E) (Uutela, 1990; Salonen, Eriksson and Gronlund, 1992), the Tswaing crater, South Africa (Partridge *et al.*, 1993), the Steinheim crater, Germany (48° 41' N, 10° 04' E) (Schweigert, 1993) and the Bosumtwi crater, Ghana (e.g. Hall, Swaine and Talbot, 1978). Often these paleolacustrine records are unique in that they owe their existence to the anomalous topographic basin represented by the impact craters.

(iv) *Intracrater-lake biology and the potential exobiological relevance*

The possibility of finding mineralogical evidence of life on Mars and the locations where such evidence might be found are of considerable exobiological interest (e.g. Robbins and Iberall, 1991; Scott, Rice and Dohm, 1991; Farmer, 1995). As locations that may have experienced ponded water in the past, impact craters are among key candidate sites to be targeted. The identification of playa deposits in impact craters is of broad planetary interest. On Mars, 'White Rock' is the first and most conspicuous intracrater feature of relatively high albedo for which a saline playa interpretation was proposed (Ward, 1979). A number of additional candidate saline playas have been suggested subsequently, in particular in the Tyrrenia highlands (Lee, 1993). Recently, Ruff *et al.* (2000) reported on the basis of Mars Global Surveyor (MGS) Thermal Emission Spectrometer (TES) data that White Rock is probably not a playa deposit as no spectral signature associated with halite or other common salts was found. But other candidate salts cannot yet be ruled out and clay mixtures should also be considered. Other putative paleolacustrine sedimentary deposits associated with impact craters also hold strong exobiological promise (Cabrol and Grin, 1995). In particular, Gusev crater (Mars, 14° 42' S, 184° 30' W) and its associated deltaic-like floor formations have received attention as potential sites of study (Cabrol, Grin and Dawidowicz, 1996).

In terms of developing a sequential protocol for the search for fossilized microbial communities in impact craters on Earth which might possibly be applied to a search for past life on Mars, four priorities can be recognised that represent successive levels of logistical difficulty. Firstly, exposed microbial fossils associated with the crater rim and putative ancient lake shores could be sought. The 14 Ma-old algal tufa deposits of the Ries impact crater, Germany (Riding, 1979) are an example of phototrophic algal biotas associated with impact lake edges. The tufa formations are relatively well exposed and easily accessible because they were associated with some of the highest water marks at the edges of the impact basin, where they remain today. Secondly, thicker sections of exposed playas and paleolacustrine sediments can be examined for biomineralogical signatures of life. If the playa/sediment surfaces do not show demonstrable signs of biomineralization, then a third step might be taken: the paleolacustrine deposits might be cored. An excellent analog for this approach is the work undertaken at Lappajärvi, Finland. Proterozoic acritarch microfossils were identified in drill cores from the lowest pre-impact sedimentary layers of the 77 Ma-old Lappajärvi impact structure at a drill depth of between 74.35 and 92.40 m (Uutela, 1990). They are well preserved compared to the microfossils in the deeper target gneiss that underlies the impact structure. Simple 7–416 μm *Leiosphaeridia* spp. dominate the low diversity fossils. At Haughton also, the permafrosted paleolacustrine deposits were successfully drilled in several locations down to approximately 10 m depth in the course of a technology demonstration for drilling on Mars. Well preserved core samples were extracted which capture the varve-forms preserved in the post-impact fill sequence. Similar shallow drilling methodologies might be used to core impact sites on Mars. Finally, if this strategy also proves unsuccessful then as a fourth step, deep drilling might be used to search for biological signatures possibly associated with the phase of thermal biology at the contact interface between the lake deposits and the underlying heated target rock as described in earlier sections. At Haughton, because the preserved paleo-lakebeds are relatively thin, the contact between the sediments and the allochthonous 'breccia' unit was encountered in the course of even the shallow drilling performed in 1998. Rather than a clear-cut contact, a disturbed mixing boundary was found that spanned a vertical thickness in excess of 1 m.

*(b) Recolonization on land**(i) The hydrologic impact oasis*

The topographic depression and enclosure associated with an impact structure in many cases results in a richer biota inside the crater. There are two principal reasons for this. Firstly, water is preferentially trapped in the crater, providing vegetation with an advantage compared to vegetation outside the crater. This occurs following rain or snowmelt or it can result from episodic variations in the level of the groundwater table, as has been suggested for Wolfe Creek crater, Australia (19° 10' S, 127° 48' E) (Shoemaker and Shoemaker, 1988). Secondly, the crater basin provides a shelter for organisms, protecting plants from wind and creating some shade in instances where the basin is deep enough.

Thus, the vegetation cover in a crater is often significantly greater than in outlying regions, particularly in biomes that are inherently depauperate immediately outside the crater. This results in an 'impact oasis'. The expression of the impact oasis will depend upon the topographical characteristics of the crater. Thus, some craters will show a concentric circular pattern such as Zhamanshin crater, Kazakhstan (48° 20' N, 60° 58' E) in which the vegetation and soil types are in well-defined locations according to the various internal structures and drainage network patterns (Burba, 1997). Where several small craters are involved, such as at the Henbury crater cluster, Australia, several distinct crater floor oases may be created. Other larger, complex, structures such as Haughton, where fluvial and glacial erosion of the paleolacustrine deposits are superposed to current meanderings of meltwater streams and the presence of irregular 'breccia' units, will tend to possess a more non-uniform ecological arrangement (Cockell *et al.*, 2001 *b*). Indeed, more so than topography *per se*, one of the most important factors determining the sequence and character of succession will be the characteristics of the exposed substratum in the impact basin. Vegetation anomalies may also be created outside craters. They will be discussed later.

(ii) Recolonization on a paleo-lacustrine substratum

In cases where an impact lake initially formed in the crater, there will be two distinct phases of post-impact succession. Firstly, the recolonization in the lake itself, and a second phase of primary succession in exposed lake sediments following the disappearance of the lake, for instance subsequent to impact

rim breaching, as might have occurred at Haughton (Hickey *et al.*, 1988).

As in volcanic succession, seeds, rhizomes and vegetative parts of plants might not be readily available at the impact site and would have to be blown in, washed in, or brought into the sediments by outlying fauna. However, following the departure of lake waters, paleolacustrine sediments will typically provide a rich substratum for vegetation that as a result of the previous overlying water column and limnetically derived sedimentation may be organically richer than many volcanic substrata (Del Moral and Wood, 1993).

Similarly to plants that colonize volcanic substrata (Uhe, 1988; Shiro and Roger, 1995), the paleolacustrine substratum is likely to be colonized by plants with effective dispersal mechanisms and a high stress tolerance for the new substratum conditions. On some volcanic substrata, succession displays a microbial and cryptogamic (lichens, mosses, etc.) phase prior to plant succession, since these more simple organisms may help in ameliorating and modifying the soils, for example on the Kula volcano in Turkey (Oner and Oflas, 1977), which showed distinctive phases of cryptogamic succession. However, it is likely that the organically enriched paleolacustrine deposits in certain impact craters will support plants at the earliest stages of succession that are blown in from outlying biomes. This will be analogous to volcanic succession on substrata where organic aeolian fall-out can support vascular plants prior to microbial enrichment, such as regions of the Mount St. Helens fall-out zone (Del Moral and Wood, 1988).

In some biomes, the process of competition for light begins with small shrubby plants leading to taller plants and eventually trees with higher canopies in arborescent biomes (e.g. Attiwill, 1994; Vester and Cleef, 1998). Such a temporal sequence of succession, which is typical for arborescent biomes, is found in the volcanically active Krakatau group of islands in Indonesia (Tagawa *et al.*, 1985) and may have occurred in some impact craters such as at the tree-filled Brent Crater, Ontario, Canada.

The biologically productive areas of the paleolacustrine sediments (Haughton Formation) at Haughton Crater represent a paleolacustrine oasis (informally named the 'Lowell Oasis'). Because of the climatic changes that have occurred at Haughton since the formation of the lake (Hickey *et al.*, 1988) it is unlikely that the present-day vegetation can provide true insights into the climax vegetation that resulted from succession after lake breach. However,

its biological productivity does provide some insights into the potential of some lacustrine sediments as substrata for recolonization, particularly when they are also associated with an impact-induced hydrologic depression.

The Haughton impact structure today lies in a typical High Arctic setting, well above the timberline. The mean annual temperature averages -16 to -19 °C with mid-June to mid-August temperatures averaging $3-6$ °C (e.g. Bliss *et al.*, 1994). The Haughton Formation is a lowland area within the impact structure. The area lies approximately 200 m below the upland surface, which is defined by the subhorizontal surface of the plateau (Allen Bay Formation) surrounding the crater. Because of its situation on the crater floor, the crater basin receives meltwater run-off during spring and summer arctic thaw. This provides the area with more favorable hydrological conditions compared to other high arctic sites, similarly to the improved hydrologic regime associated with some arctic oases (unrelated to impact craters) on Devon and Ellesmere Islands (Svoboda and Freedman, 1981; Bliss, Svoboda and Bliss, 1984; Thomas and MacDonald, 1985; Muc, Freedman and Svoboda, 1989; Bliss *et al.*, 1994). Grass and sedge meadow type areas are a typical feature of the Lowell Oasis area at Haughton and in terms of vegetation, many areas resemble the Truelove lowlands of eastern Devon Island (Bliss, 1977). The vegetation cover across much of the formation lies between 20 and 90%. From our 1997 and 1998 field observations, it is clear that these Haughton meadows can support microtine populations, particularly collared lemmings (*Dicrostonyx groenlandicus*). Larger vertebrates include musk-ox (*Ovibos moschatos*), Perry caribou (*Rangifer tarandus*), and arctic hare (*Lepus arcticus*), birds such as rock ptarmigan (*Lagopus mutus*), snow bunting (*Plectrophenax nivalis*) and snowy owl (*Nyctea scandiaca*), and charismatic megafauna such as polar bears (*Ursus maritimus*). This main paleolake sediment outcrop area is conspicuously more productive than other regions outside the crater and might tentatively be defined as a polar oasis.

(iii) *The salt pan oasis*

While impact craters generally serve as hydrological basins, those in arid environments may experience significant evaporation and/or underground drainage as well. The departure of an intracrater-lake then results in the formation of a playa deposit. Such deposits may be found resting on top of a

sequence of intracrater sediments, or they may be interbedded in the latter if more than one lacustrine episode with an evaporative phase occurred. In the Tswaing crater, South Africa, a 1.13 km diameter impact crater, a playa deposit is exposed around the edges of the hypersaline impact crater-lake. The lake has a salinity of 10–40% depending on depth (Ashton, 1999) and around the edges of the lake are microbial mats. A salt-tolerant sedge, *Scirpus maritima*, grows in and around the feeder streams into the lake (Ashton, 1999). Hot desert conditions generally make good examples of impact craters with intracrater salt pans and associated vegetation stands. The Australian Outback, for instance, holds several craters with playa units on their floors (Shoemaker and Shoemaker, 1988). At Wolfe Creek crater (Fig. 6A) stands of vegetation occur inside a 0.87 km-diameter crater on the crater's playa deposit that are richer than in some of the outlying regions (Reeves and Chalmers, 1949; Cassidy, 1954). Numerous run-off gullies carved by water draining into the crater can be seen along the crater rim. Crater number 7 at the Henbury craters, Australia ($24^{\circ} 34' S$, $13^{\circ} 38' E$) is the largest of this cluster of craters (180 m \times 140 m) and also possesses a small playa exhibiting small stands of conspicuous vegetation (Fig. 6A). Drainage around the Connolly Basin, Australia ($23^{\circ} 32' S$, $124^{\circ} 45' E$), converges radially towards the center of the basin where spiny spinifex grows (Hodge, 1994). Impact craters in deserts on other continents display similar features. The Monturaqui crater, Chile ($23^{\circ} 56' S$, $68^{\circ} 17' W$) located in the hills lining the southern end of the Atacama desert has gullied walls and a bright, off-centre clay and silt playa deposit on its floor (Sanchez and Cassidy, 1966). The few brushes that grow on the crater floor are associated with the playa deposit, probably because this particular location experiences preferential water collection. The salt-pan impact oasis can be considered a rather specialized impact ecosystem associated with arid desert-like environments subjected to short periods of precipitation. Often, the salt gradient created in simple craters with significant evaporation will display strongly concentric characteristics.

(iv) *Recolonization on impact-generated and other non-lacustrine substrata*

In cases where a crater-lake does not form, non-lacustrine intracrater substrata can still support a vegetation anomaly at the crater. Two of the Ilumetsy craters, Estonia ($57^{\circ} 58' N$, $27^{\circ} 25' E$) have

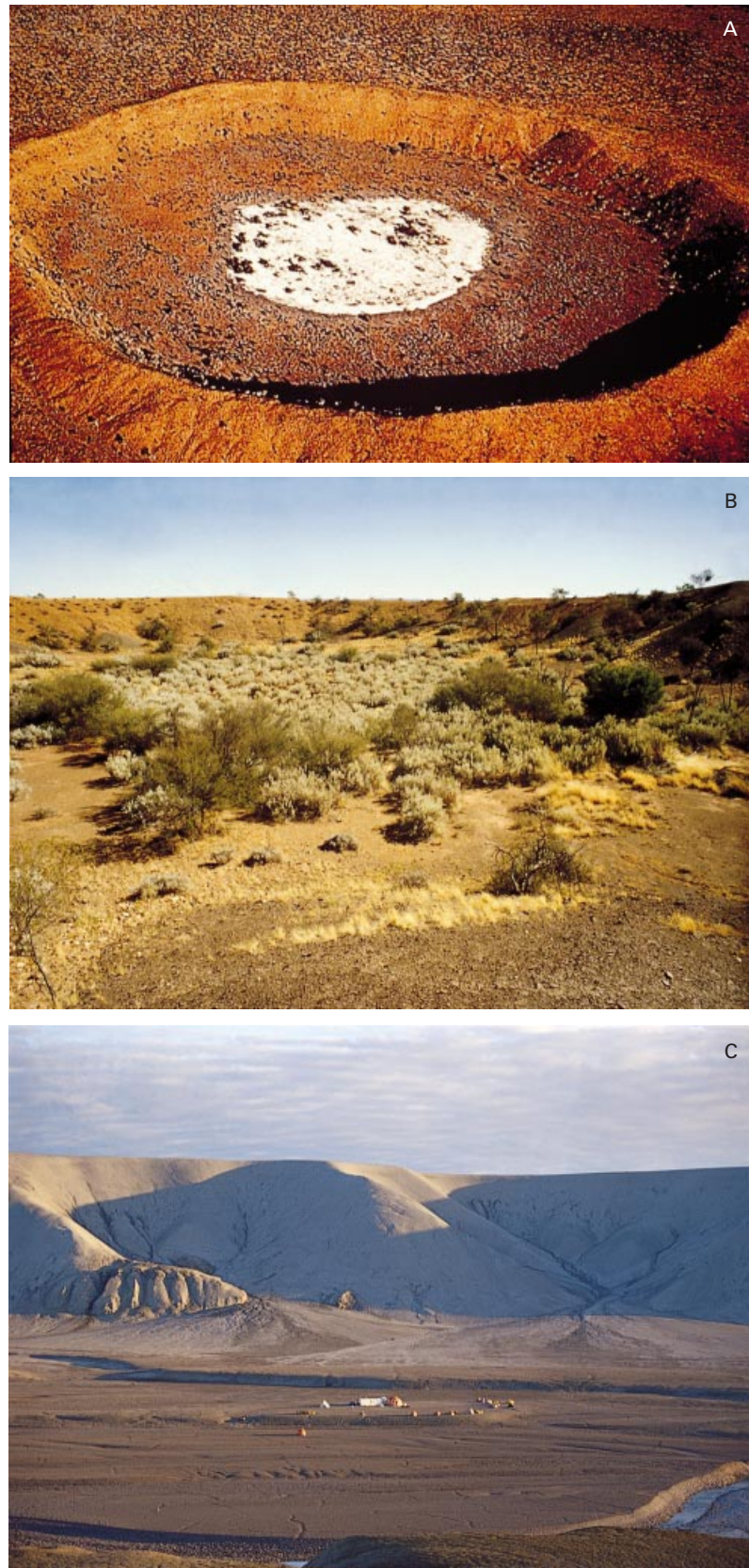


Fig. 6. The 0.87 km diameter Wolfe Creek impact structure in Australia (A). The impact crater is the site of a salt and clay rich playa. Henbury crater number 7 (B), less than a quarter of a kilometre in diameter, is an example of



Fig. 7. 'Micro-oases' on impact breccia (A) and alluvial terraces (B). The micro-oases are small features of high biological productivity in the otherwise depauperate polar desert of the Haughton impact structure. The formation of the features on the breccia represents a generalized process for the colonization of an impact substratum that bears some similarities to observed processes of colonization on Mount St. Helens volcano involving burrowing animals. The size of the bars is 60 cm (photographs, Charles Cockell).

become infilled with large amounts of peat, in contrast to their immediate surroundings. Some craters may accumulate aeolian or glacial drift, which may or may not result in an intracrater substratum attractive to vegetation. In cases where sand does not favour vegetation (because of the sand's composition or the constant aeolian activity), the crater may actually become slightly more depauperate than the outlying regions. Such appears to be the case of Amguid, Algeria ($26^{\circ}05' N$,

$4^{\circ}23' E$), which is filled with fine white sand, and also of Roter Kamm, Namibia, which is filled with sand from the Namib Desert (Fudali, 1973). In the case of smaller craters where an initially pronounced topographic anomaly reduces to a subdued pedologic disturbance, a local anomaly in the vegetation cover may become the clearest surface expression of the craters themselves. An interesting example of vegetative recolonization in such a case may be found at the Rio Cuarto structures, Argentina ($32^{\circ}52' S$, $64^{\circ}14' W$). There, several oblong depressions, some of which are a few kilometres long and approximately 250 meters wide, are interpreted as resulting from a multiple side glancing impact event (Schultz and Lianza, 1992). For some of these craters, the main distinguishing feature at present is a vegetation anomaly, probably due to reworking of the topsoil and perhaps a different nutrient content (Schulz and Lianza, 1992) associated with the hydrologic basin factor.

Sometimes the crater rim gives rise to stands of thicker vegetation, in some cases even thicker than at the center of the structure. Two possible causes can be invoked. Higher concentrations of evaporitic salts near the center may make the area less attractive biologically to halophobic species, and/or the topographic high represented by a crater rim may make it a site favoured by enhanced aeolian deposition or by landing birds whose droppings can then enrich rim materials in nutrients. At Meteor Crater for instance, in addition to a scattering of juniper trees that may be up to 700 years old on the crater floor and the rim area (Smith, 1996), a 40° arc of cedar trees also lines the crater's south-southeastern rim. The presence of these conifers is rendered possible by the local accumulation of windblown sand. Enhanced rim vegetation is also seen at Boxhole crater, Australia ($22^{\circ}37' S$, $135^{\circ}12' E$). At the Veevers structure, a small 0.08 km-diameter impact crater also in Australia ($22^{\circ}58' S$, $125^{\circ}22' N$), small trees have preferentially grown along the edges of the crater wall in an otherwise desolate environment (photographic observations).

The patterns of vegetation on land in an impact crater can additionally be strongly influenced by the presence of impact-generated lithic substrata

the preferential growth of vegetation in the hydrologic depression caused by a crater. (C) The breccia hills of the 24 km diameter Haughton impact structure near to the base camp (1997–1999) of the Haughton-Mars Project were the subject of microbiology and vegetation studies described in the text (Cockell *et al.*, 2001*b*) (photograph, Charles Cockell).

such as impact breccia or impact melt. On exposed impact-generated units the patterns of ecological succession are unlikely to be similar to those associated with lacustrine deposits. There are two principal physical reasons for this. Firstly, the impact event will tend to destroy the organic and nutrient-rich topsoil that might have existed at the target site before the impact. As well as the resulting bulk displacement of the target materials, the impact-generated crater fill will also be rendered biologically oligotrophic by the heat of impact. This will occur by the impact-volatilization of biologically important nutrients and minerals. Many important biological minerals will volatilize at temperatures well below those encountered during impact. For instance; nitrogen, 200 °C; organic phosphorus, 350 °C; inorganic phosphorus, 750 °C; sulphur, 450 °C; potassium, 570 °C; sodium, 880 °C. In this respect there are interesting parallels with soil impoverishment processes associated with fire ecology, particularly at the site of high-intensity forest fires where volatilization of essential biological minerals occurs (e.g. Agee, 1993). Secondly, patterns of zonation in vegetation often follow geological patterns, because of the associated pH and nutrients of underlying soils. In the case of Haughton, the target rocks are dominated by carbonates, which are alkaline. Thus, although the impact breccia unit at Haughton contains some quantities of basement gneisses and other excavated rocks, the carbonates determine the impact-generated unit's pH characteristics. For this reason, the impact breccia at Haughton is colonized by *Salix* spp., *Saxifraga* spp., grasses and other flora that are similar to those found in outlying areas inside and outside of the crater (Cockell *et al.*, 2001*b*), but in covers much smaller than over the paleolacustrine units of the Haughton Formation.

The degree of thermal processing experienced by impacted rocks will affect colonization. Where melt layers are exposed, recolonization by plants will be rendered more difficult where the igneous rocks are denser.

The impact breccia found in the Haughton impact structure is of particular interest with respect to the mechanisms of post-impact succession (Fig. 7) (Cockell *et al.*, 2001*b*). In most regions of the crater, the low nutrient composition of the soils, the periglacial processes and extreme winter and summer temperatures render the ground biologically depauperate. The mean vegetation cover on the breccia was 0.1%, compared to 6.1% on the alluvial terraces of the Haughton River (Cockell *et al.*,

2001*b*). The lower vegetation cover on the breccia compared to the river terraces was attributed to the coarse structure of the breccia and the high breccia hills, which more readily lose moisture than the river terraces that are fed with water from the Haughton River.

The allochthonous impact breccia ecologically now resembles typical polar desert/semi-desert (Fig. 6C). The low nitrogen and phosphorus content of the breccia is typical of soils of the High Arctic (e.g. Walker and Peters, 1977; Bliss *et al.*, 1984; Henry *et al.*, 1986; and references therein). The breccia is inhabited by rather low diversity flora (typical species richness of 5) which include isolated colonies of *Papava radicum*, *Eriophorum* spp., *Salix* spp., *Draba* spp., *Saxifraga* spp., and some grasses such as POA spp. and *Alopecurus* spp. which are typical for this region (Shulten, 1975).

An input of organics or nutrients may provide the mechanism for a localized increase in biological productivity. This is observed in small 'micro-oases' (typical sizes < 400 cm in diameter) that are found on the alluvial terraces and breccia deposits within the impact structure (Fig. 7). Many of them have developed into lemming mats, similarly to those observed on beach ridges elsewhere on Devon Island (Mallory and Boots, 1983). In the micro-oases at Haughton, a high vegetation cover, between 2 and 98% cover, attracts collared lemmings and birds, which provide further nutrient input (Cockell *et al.*, 2001*b*). A positive feedback process is generated resulting in a localized area of enhanced productivity. The formation of these areas is assisted by some physical processes such as the presence of ground stabilizing rocks, similarly to the role that rocks can play in providing habitats for seedlings on volcanic substrata (Wood and Morris, 1990). Similarly to the polar desert, the breccia micro-oases have a lower vegetation cover compared to the alluvial terrace micro-oases.

The processes observed at Haughton are similar to the re-invasion of the volcanic tephra produced by the 1980 eruption of Mount St. Helens in the USA. In this case, northern pocket gophers (*Thomomys talpoides*) formed mounds on the volcanic tephra which resulted in areas of greatly enhanced plant productivity, presumably due to re-working of the old soil to the top (Andersen and McMahan, 1985). Thus, as with volcanic primary succession, the lemmings of Haughton suggest a potentially important role for burrowing animals in accelerating succession on impact substrates (Cockell *et al.*, 2001*b*).

(v) Climax ecology

Ultimately, the biota in a crater will reach some type of equilibrium that is recognized as a 'climax ecosystem', where species turnover is substantially reduced and the number of fugitive species is also reduced compared to the first stages of colonization (of course, as with all discussions on this subject it should be understood by the reader that the concept of a post-impact 'climax' is specious, because in reality turnover of species can be occurring at all times. Nevertheless the climax period is a useful concept broadly to separate the period when the crater is undergoing rapid change and species replacement after the impact event as new substrata become available, and the periods when the ecology is relatively stable). The crater may well remain very distinct from the outlying biomes (such as with the Lowell Oasis on the Haughton Formation and its ecology). Thus, this stage of climax is distinguished from ecological assimilation, which is discussed in Section III.3. Climax ecology will occur when the biological patterns of change and geological rearrangements occurring inside the structure have stabilized, but geological features of the crater (such as the presence of a hydrological depression or the exposure of impact breccia) still make the ecology different from areas outside the crater. Although the climax ecosystem may be long-lived (greater than millions of years), a further geological re-arrangement, for example the breach of a crater rim resulting in the drainage of a crater lake or the erosion of a breccia unit to the target rock below it can initiate a new phase of recolonization and impact succession. Thus, the climax ecosystem may be transitory.

(vi) Impact-induced fertilization?

Whilst recolonization of vegetation will depend critically upon water availability and the characteristics of the substratum, it is possible that impact processes may alter the recovery of vegetation in the immediate area around the impact site by changing the nitrogen cycle. Shock-induced gas-phase reactions in the atmosphere during bolide entry can synthesize nitric oxide, which in turn may react with atmospheric oxygen to form fertilizing nitrogen compounds (Melosh, 1989; Zahnle, 1990). Following the 1908 Tunguska event, where an estimated 3×10^{10} kg of nitric oxide was produced by the shock wave accompanying the meteor (Turco *et al.*, 1982), forests surrounding the event site experienced unprecedented rates of growth (e.g. Boslough, 1991).

These increases in growth rates are reflected in tree ring widths (Longo, Galli and Serra, 1996). Although the fires in the region might have opened canopy space and improved growth rates, a nitrogen isotope anomaly at the Tunguska site does suggest an abiotic nitrogen input into the region at the time of impact (Kolesnikova *et al.*, 1996).

As well as impact-induced nitric acid formation, fires with surface temperatures exceeding 200 °C also volatilize nitrogen (as could direct impact-induced heating in the area of the impact crater). Although high-severity fires can cause net reductions in nitrogen capital through volatilization, they also tend to increase the concentrations of biologically available ammonium-nitrogen and more mobile nitrate-nitrogen (Agee, 1993). Thus, it is conceivable that at the site of impact, shock-induced synthesis of nitric acid and fire processes could cause a transient increase in growth rates coupled through the nitrogen cycle. For ecosystems in which plants are nitrogen limited, this process will clearly be of importance for determining patterns of post-impact growth, although in biomes where plants are not nitrogen limited, then the effect of an increase in biologically available compounds would be limited. The generality of this process is not known, but it represents a potentially important impact-induced ecological effect.

(c) The ecotone surrounding the impact site

Although this review primarily concentrates on the impact crater, it is important to remember that the area around the impact crater may also become a site of primary or secondary succession, the latter being the case for less disturbed areas further from the site. In Section III.2b(iv), rim area effects were discussed. More distant effects are possible, however. In ecosystems with high fuel loading, such as shrubby ecosystems in arid regions, impact ejecta could ignite fires in the local area around the site, which would be exacerbated by direct impact heating. Furthermore, the airburst and intense surface blast wave believed to accompany impacts will also affect the biota. Kring (1997) estimates that severe damage to forests may have occurred up to 20 km from the site of the Meteor Crater in present-day Arizona and animal fatality may have occurred up to 4 km from the site. Dead trees and animals would provide nutrients for new vegetation. Grass and some low-lying plants might survive in some areas around the site and in general, the topsoil will be preserved. However, together with impact fires, a charred

ecotone of alteration will occur around the site of the impact event with decreasing severity of ecological change further from the impact site. The radial distance of this ecotone will of course depend upon the energy of the event, which can be approximated using scaling methods (e.g. Glasstone and Dolan, 1977).

(d) *Recolonization and succession in pelagic impact events*

In the case of pelagic impact events the destruction of the benthic biota will initiate a period of recolonization and succession involving algae, marine invertebrates and eventual invasion by marine vertebrates which may be similar to other natural and human-generated benthic disturbance events (Rosenberg, 1976; Arntz and Rumohr, 1986). As in the case of land impacts, the disturbance of benthic marine sediments and the resulting nutrient and mineral arrangements will determine the patterns of ecological succession. A good example of a shallow-water marine impact is the Montagnais impact crater, Canada (42° 53' N, 64° 13' W), which occurred in water of approximately 600 m depth. Examination of the site shows that the crater rim may have been significantly eroded since the impact 51 Ma ago (Jansa and Pe-Piper, 1987; Jansa, 1993). Much of the associated reformed breccia-like material is re-worked into the crater by return water flow into the cavity where it forms thicker layers than in land settings. Because of the return water flow into the crater, sedimentary deposition into the basin will continuously cover benthic habitats for a period of time after impact, but by the same token, this process will also eventually bury the site of impact. Over time, an ocean bottom habitat much like the surrounding areas is restored. Indeed, Montagnais is at present in the assimilated phase (see below).

(e) *Dependence on geological epoch*

The nature of the Phase of Impact Succession will also depend upon the geologic epoch in which the impact occurs. An impact occurring in the Precambrian such as Beaverhead, Montana, USA (44° 26' N, 113° 00' W), or Sudbury, Ontario, Canada (46° 36' N, 81° 11' W), would be subject only to microbial recolonization.

A terrestrial impact in the early Devonian approximately 320 Ma ago, e.g. Crooked Creek, USA (37° 50' N, 91° 23' W) would be limited to plant and insect recolonization on exposed land, but a pelagic impact in the same epoch would be subject to

patterns of succession involving vertebrates. Thus, patterns of succession in impact craters must have depended upon geologic epoch.

Large-scale impacts capable of altering the environment on a global scale may themselves herald a new geologic epoch. While the exact mechanism whereby the dinosaurs and other genera became extinct at the Cretaceous–Tertiary boundary remains unclear, the geologic transition itself may have been triggered by the Chicxulub, Mexico, impact event (e.g. Hildebrand *et al.* 1991).

(f) *Recolonization after changes in the global environment*

After large-scale impact events (approximately $> 10^5$ – 10^6 Mt), the biota surrounding the impact crater will itself be disturbed, not through the impact directly, but through the indirect effects of global environmental disturbance. Reductions in insolation and temperature have been proposed as global environmental effects of large-scale impacts (e.g. Toon *et al.*, 1997; Cockell and Stokes, 1999). Global wildfires, tsunamis and increases in UV-B radiation following dust and soot clearing might also compound the biological stress. Following these effects a global phase of succession will occur. The outlying process of succession might itself affect, for instance delay, the recolonization of the impact crater.

(g) *The impact crater as a biogeographical island*

Some features of impact craters conform to ideas of insularity and characterize the impact crater in some respects as a biogeographical island. In the case of impact craters with lakes, once autotrophic communities have been established in the lakes, higher trophic levels such as fish populations become established that, because of physical and genetic isolation, become highly derived and eventually completely endemic to the crater-lake. This has been reported at the El'gygytgyn crater, Russia (Skopets, 1992). It was also reported that this was the case at the New Quebec crater, Canada, although a single population of arctic char (*Salvelinus alpinus*) inhabits the lake (Gronlund *et al.*, 1990, Richard, Bouchard and Gangloff, 1991) that does not appear to be endemic (although it could plausibly be distinguishable by genetic fingerprint analysis from outlying populations). The same phenomenon is also suggested from the remains of endemic trout and smelt-like fish found in the Haughton Formation (Hickey *et al.*, 1988; Whitlock and Dawson, 1990), although the extent to which the Miocene fish at Haughton

might have differed from Miocene fish found in the High Arctic outside the crater cannot be assessed because there is no other record of the Miocene. Similar paleobiological evidence of endemism is found in the *Gyraulus* spp. snails of the Steinheim impact crater sediments (Reif, 1983; Gorthner, 1992).

As well as endemism in the aquatic realm, some physical features of craters offer potential for isolation in the terrestrial realm. A few impact structures possess small islands within the intra-crater-lake. The islands are generally expressions of either a central uplift (e.g. Gow crater, Saskatchewan) or an uplifted inner ring (e.g. Clearwater West, Quebec). As for any island, impact crater islands might possess biotas that are genetically distinguishable from outlying regions.

The biogeographical boundary of the crater rim might be a significant isolation factor for small flightless terrestrial invertebrates and vertebrates, and possibly also for plant communities with inefficient dispersal mechanisms. The Serra da Cangalha impact structure, Brazil (8° 05' S, 46° 52' W), in which an almost perfectly circular ring of uplifted hills some 250 m high isolates a 'hidden valley' at the center of the structure, and Gosses Bluff, Australia (23° 50' S, 132° 19' E), which is similarly outlined by a ring-shaped mountain range, represent two candidate examples worthy of examination.

The evolution of species that are endemic only to the impact crater habitat is unlikely, unlike the case with volcanism. Because volcanism may be sustained in particular locations for long periods of time, some organisms specifically evolve to fit the post-volcanic primary succession habitat. It is estimated that there has been exposed new lava flows and post-volcanic forest in Hawaii at any one time somewhere in the islands for the past 70 million years (Thornton, 1984; Thornton *et al.*, 1990). Some species of arthropods inhabit lava fields, living off aeolian biological fall-out. Once vegetational succession begins, these species become extinct in the habitat, suggesting specific adaptation to the post-volcanic environment (Thornton *et al.*, 1990). They, as for forest animals, transfer from island to island over geologic time periods, living in newly available volcanic primary succession habitat. By contrast, the temporal spacing of impact events and their spatial distribution across the surface of the Earth in many biomes means that it is improbable, and perhaps even impossible, that a functional niche exists for a species that exclusively utilized the post-impact

succession environment. Most species that recolonize impact craters will be opportunistic species from the immediate outlying regions. Of course, on early Earth, when the impact flux was higher, craters may have been a more common habitat. Transfer of microbes, such as those that opportunistically take advantage of hydrothermal environments (which are now confined to volcanic geothermal areas such as Yellowstone National Park, USA), may have been more common.

(h) *Human interactions – an unusual type of recolonization and succession event*

For completeness the interactions of humans with impact craters should not be overlooked as human settlement is a form of biological incursion. Many human interactions with impact structures have not been documented in the scientific literature and hence much of the evidence available is anecdotal. Here, a selection of interactions is described that have relevance to the biological processes described in this paper.

The use of impact craters by humans has gone back millennia. The Tswaing impact crater in South Africa appears to have been visited, albeit not permanently settled, since the event itself. Stone tools in the crater provide evidence that Middle Stone Age people visited the crater between 150 000 and 30 000 years ago, perhaps to collect salt (Reimold *et al.*, 1999). The crater ring wall of the Lake Kaali structure was inhabited by Bronze Age man approximately 4000 years ago (Saarse *et al.*, 1991).

Because of the hydrologic advantages and, in many cases, the paleolacustrine deposits they offer, impact craters have often been attractive to humans for their agricultural potential. Preferential agricultural activity has occurred in the 3.8 km-wide Steinheim crater in Germany, compared to outside (e.g. Reif, 1983). Farms take advantage of the sediments and flat land of the Bigach impact crater in Kazakhstan (48° 30' N, 82° 00' E). Although now ploughed over for farming, in 1925 the Haviland crater, Kansas, USA (37° 35' N, 99° 10' W), a small 15 m diameter crater, was used as a drinking hole for farm animals because the crater held water for longer than many of the buffalo wallows in the local area. The 23 km diameter Lappajärvi impact lake, Finland (63° 12' N, 23° 42' E) has been surrounded by many fertile farms which farm rye, wheat and potatoes. The 24 km Ries impact structure, Germany is covered in prosperous farms and offers yet

another outstanding example of human activity. The walled city of Nordlingen, which was built in the basin, has a church constructed from impact breccia, similarly for the manor house in the Rochechouart impact structure, France (45° 50' N, 0° 45' E). In some cases, impact structures have been a hindrance to agriculture. An example is the Rio Cuarto side-glancing impact structures in Argentina, where the depressions and rough edges have actually been avoided by farmers (Schultz and Lianza, 1992).

Throughout history, humans have often built towns and cities in strategically and economically attractive places. The agricultural richness of impact basins and the often flat, plain-like characteristics of the central areas of the structure make impact basins attractive as locations for long-term settlement. The Middlesboro impact structure, Kentucky, USA (36° 37' N, 83° 44' W), is a conspicuously flat area amidst the surrounding mountains and steep stream valleys (Englund and Roen, 1962). As a result of this topography it now hosts the city of Middlesboro. The lake and tourist activity is the reason for the existence and growth of the town of Lappajärvi, Finland. The south-east of the Lappajärvi impact structure rim is steep and has been used for a ski resort. A ski lift is constructed on the impact rim. Both Middlesboro and Lappajärvi are two of the few examples of cities that have developed and grown as a direct result of advantages offered to humans by an asteroid or comet impact crater.

The geological disturbances associated with craters often result in the exposure of rocks that have commercial value (Grieve and Masaitis, 1994). The three central uplift hills of the Glover Bluff impact structure, USA (43° 58' N, 89° 32' W) have been used to mine dolomite of lower Ordovician age, the hills providing easier access. Quarrying has also occurred in the Kentland impact structure, Indiana, USA (40° 45' N, 87° 24' W). The Sudbury impact structure, Ontario, Canada contains the world's largest nickel-copper sulphide deposits and is thus of considerable economic importance. Over 15 million tons of nickel and copper have been mined from the structure. The Vredefort structure, South Africa (27° 00' S, 27° 30' E) is associated with one of the world's largest gold depositories.

Other economic benefits can be derived from impact structures. The Odessa impact structure, Texas, USA (31° 45' N, 102° 29' W), was seen to have commercial advantage by the local council, who apparently used it as a local dump. Great commercial value has been obtained from the salt deposits of the Tswaing impact crater. Reimold *et al.*

(1999) provide a nice review of the history of Tswaing and its salt deposits.

The possibility of natural gas being trapped in the disturbed rocks of impact craters was spectacularly demonstrated one night in November 1956 when a drill rig built in the Holleford impact structure, Canada (44° 28' N, 76° 38' W) exploded when the borehole reached 60 m. The release of gas changed the pressures and hydrology beneath the impact structure such that water no longer came to the 35 m deep drinking well of the farmer who inhabited the crater. The Siljan impact structure, Sweden (61° 02' N, 14° 52' E), was also drilled for natural gas, although no gas was found. The Avak structure, Alaska (71° 15' N, 156° 38' W), has little surface expression, but is the site of natural gas mining.

There are also many examples scattered through history of peoples using meteoritic iron and other materials from impact structures for the manufacture of jewelry and tools.

Finally, the vagaries of human behaviour have resulted in copious myths and legends. Because of the deep impact crater-lake (average 200 m depth) found in the Deep Bay impact structure, Saskatchewan, Canada and the lack of islands, the waters are dark and prone to being treacherous during storms. This is in contrast to the nearest lake, Reindeer Lake, which is only 30 m deep and full of islands. Unsurprisingly, the lake has developed a negative reputation amongst the local people, who believe that the lake is inhabited by a giant fish with habits and behaviour similar to the famed Loch Ness monster in Scotland. During winter the legend states that the beast breaks through the crater-lake ice and devours tender young caribou. Similar stories of monster fish have pervaded the towns near the New Quebec crater-lake, Canada. However, serious studies show that the size distribution of the arctic char in the lake is normal, although the fish do have cannibalistic habits (Gronlund *et al.*, 1990). The involvement of impact craters in popular literature and science fiction could be exhaustively discussed. However, in terms of direct involvement of a terrestrial impact structure, perhaps the most famous is Wolfe Creek, Australia which is the location of a mystery novel by Arthur Upfield written in 1934 and entitled 'Death of a Swagman' (Upfield, 1934).

(3) Phase of Ecological Assimilation

Eventually, the ecology of the impact crater will start to become similar to the outlying regions of the crater such that the crater will ecologically become

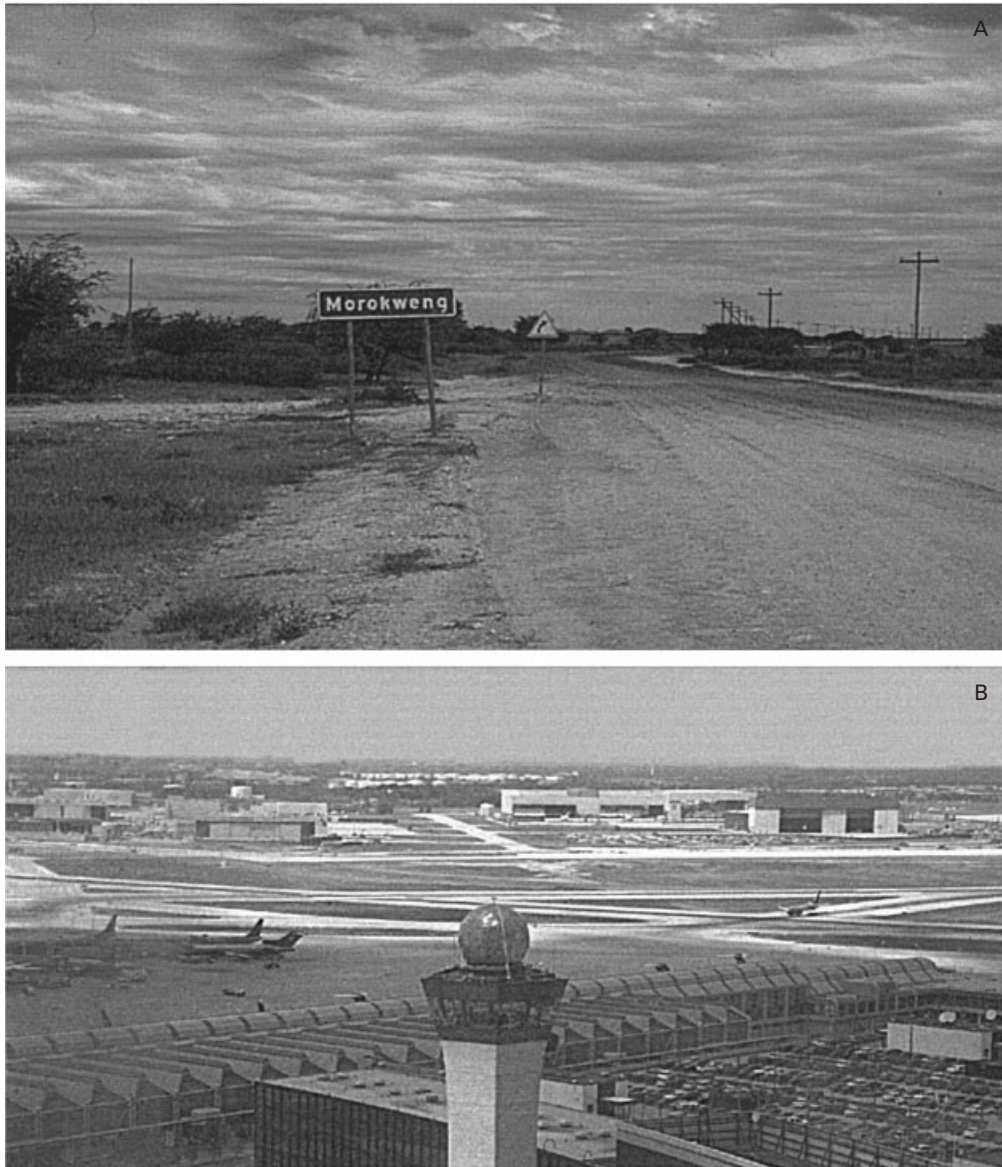


Fig. 8. Craters in the Phase of Ecological Assimilation. Site of the Morokweng impact structure, South Africa (A). The 70 km diameter crater is buried beneath the town of Morokweng on the edge of the Kalahari desert and it is an extreme example of a crater in the Phase of Ecological Assimilation, where the ecology of the crater is indistinguishable from the outlying region (photograph, Charles Cockell). O'Hare International Airport (lower) partially overlies the 8 km diameter Des Plaines impact structure in the USA and it was discovered by engineers building tunnels for the airport. It is an example of assimilation which has been furthered by human activity (photograph, NASA Ames Home Page).

assimilated into the surrounding biome and is no longer signaled by a biological anomaly. We can refer to this as the Phase of Ecological Assimilation and we might define it as the point at which the ecology of the crater site becomes indistinguishable from that of outlying regions. A feature of this phase is that the ecological uniqueness of the crater site tends to be lost as the geological distinctiveness is lost.

Where a crater lake has formed and then the crater rim was breached, the lake may become assimilated into external water bodies and thus loses its biological isolation [e.g. Nicholson lake, Northwest Territories, Canada ($62^{\circ} 40' N$, $102^{\circ} 41' W$)]. Care has to be taken in defining a crater containing a lake as 'assimilated', because although the lake might be connected to outlying water bodies, the unusual depth of some crater lakes (e.g. the New

Quebec crater, Canada) might allow them to retain some characteristics that are made possible specifically by geological characteristics still expressed by the impact structure.

Where craters do not contain lakes, assimilation will occur when the structure becomes eroded or infilled to a point where the depression no longer results in a distinct intra-crater vegetational anomaly. The Campo del Cielo craters, Argentina (27° 38' S, 61° 42' W) were assimilated into local forests and shrub. Slashing was necessary to examine the crater field (Cassidy and Renard, 1996).

Aerial photographs show that assimilation has occurred in a variety of impact craters, such as the Aourunga craters (19° 06' N, 19° 15' E) assimilated into the Sahara desert of Chad, Africa (although the biology of the Sahara is very depauperate) and Kelly West, Australia (19° 56' S, 133° 57' E). The phase of ecological assimilation may take a substantial length of time. Examination of present-day terrestrial impact structures shows that approximately 50% are assimilated and the other 50% contain some type of climax ecosystem that is distinguishable from the outlying biota.

The phase of ecological assimilation is likely to be achieved much quicker for pelagic impact events compared to impacts on land. The cavity in pelagic impacts will be partially filled by water back-flow and bottom water turbulence leading rapidly to a relatively stable sediment surface over the impact breccia. Marine organisms will move into the benthic habitat with greater speed than land animals move into a disturbed habitat. The Montagnais crater is now buried beneath the sea floor.

A common yet extreme case of assimilation is when the crater becomes completely buried. Morokweng crater, South Africa (26° 28' S, 23° 32' E), which is now buried under the town of Morokweng (Fig. 8A), is such an example. The Kaluga crater, Russia (54° 30' N, 36° 15' E), is also an example, being buried beneath 800 m of Devonian and Carboniferous sedimentary rocks. Obolon in the Ukraine (49° 30' N, 32° 55' E) is buried underneath 270 m of Cenozoic and Cretaceous sedimentary rocks. The 35 km Manson crater, Iowa, USA (42° 35' N, 94° 33' W), is now completely buried under the sediments of north central Iowa State (Hartung and Anderson, 1988). The Des Plaines impact structure, Illinois, USA (42° 03' N, 87° 52' W), is now located under the city of the same name (Emrich and Bergstrom, 1962), and the southwest of the structure is now overlain by Chicago's O'Hare international airport, assimilation in this

case having been furthered by human activity (Fig. 8B).

A further case of assimilation is when the crater is completely buried by ice or snow. Craters under the Antarctic ice sheet, for example, are in a phase of assimilation. The melting of the ice sheet would expose craters in which successional development could then occur, illustrating an instance of temporary assimilation by ice cover.

IV. CONCLUSIONS

(1) Asteroid and comet impact events are the only extraterrestrial mechanism that can deliver a localized pulse of destructive energy into an ecosystem. The study of the ecological characteristics of impact craters elucidates how impact events can influence change on a local level as well as the more widely studied global-scale effects. These studies can provide a valuable comparison to patterns of recovery and succession following other agents of ecological destruction that have previously been a focus of study, such as volcanoes, glacial retreat, storms and fires.

(2) Based on our review of the existing literature and our observations at Haughton and other impact structures, we recognize three phases of biological recovery following an impact event (Fig. 4).

(3) Firstly, a Phase of Thermal Biology occurs in the immediate aftermath of an impact event and is tied directly to the thermal pulse delivered to the target by the impactor. It is likely to be dominated by colonizing microbial communities, particularly those common to hydrothermal activity. This phase is of particular interest in the context of exobiology.

(4) Secondly, the Phase of Impact Succession and Climax occurs, a rather complex phase that may involve multiple episodes, including the formation and breach of an impact crater lake(s). During this phase, geological characteristics unique to impact craters such as the crater rim and bowl, the formation of impact breccia and the isolation of a crater lake are the primary influences shaping the ecological characteristics. Various stages of climax may be achieved during this phase as geological alterations occur. For example, succession and climax in a lake might be followed by a further stage of succession and climax on a paleolacustrine sedimentary deposit after the lake waters depart. This might be further followed by succession and climax as lacustrine sediments are eroded, exposing impact breccia underneath.

(5) Finally, the Phase of Ecological Assimilation is the phase during which the geological uniqueness of the crater is finally lost and with it, complete assimilation of the impact crater into the outlying biome occurs. This is often only truly reached when the crater is buried.

V. ACKNOWLEDGMENTS

Observations at the Haughton impact crater, Devon Island, Nunavut, Canada, reported in this article were conducted in the course of the 1997–2000 field seasons of the NASA Haughton-Mars Project, a field research program supported by NASA and by other government and private partners, including the National Geographic Society (see www.arctic-mars.org). Logistical support in Canada was provided in part by the Polar Continental Shelf Project (PCSP). A Research License to conduct field work on Devon Island was issued by the Nunavut Research Institute. Observations at the Tswaing impact crater were made possible with the kind collaboration of the Impact Cratering Research Group at the University of the Witwatersrand, Johannesburg.

VI. REFERENCES

- AGEE, J. K. (1993). *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington DC. pp. 493.
- ANDERSEN, D. C. & McMAHON, J. A. (1985). Plant succession following the Mount St. Helens Volcanic Eruption: Facilitation by a burrowing rodent, *Thomomys talpoides*. *American Midland Naturalist* **114**, 62–69.
- ARNTZ, W. E. & RUMOHR, H. (1986). Fluctuations of benthic macrofauna during succession and in an established community. *Meeresforschung* **31**, 97–114.
- ASHTON, P. J. & SCHOEMAN, F. R. (1988). Thermal stratification and the stability of meromixis in the Pretoria Salt Pan, South Africa. *Hydrobiologia* **158**, 253–265.
- ASHTON, P. J. (1999). Limnology of the Pretoria Saltpan Crater-lake. In Tswaing. Investigations into the origin, age and paleoenvironments of The Pretoria Saltpan (Partridge, T. C.). Council for Geoscience. Geological Survey of South Africa. Memoir 85. Pretoria. 198 pp.
- ATTIWILL, P. M. (1994). The disturbance of forest ecosystems, the ecological basis for conservation management. *Forest Ecology and Management* **63**, 247–300.
- BANDERAS TARABAY, A., GONZALEZ VILLELA, R. & DE LA LANZA ESPINO, G. (1991). Limnological aspects of a high-mountain lake in Mexico. *Hydrobiologia* **224**, 1–10.
- BARNES, S. M., FUNDYGA, R. E., JEFFRIES, M. W. & PAGE, N. R. (1994). Remarkable archaeal diversity detected in a Yellowstone National Park hot-spring environment. *PNAS* **91** (5), 1609–1613.
- BLISS, L. C. (ed.) (1977). *Truelove Lowland, Devon Island, Canada: A high arctic ecosystem*. Edmonton: University of Alberta Press, 31–62.
- BLISS, L. C., SVOBODA, J. & BLISS, D. I. (1984). Polar deserts, their plant production in the Canadian high arctic. *Holarctic Ecology* **7**, 324–344.
- BLISS, L. C., HENRY, G. H. R., SVOBODA, J. & BLISS, D. I. (1994). Patterns of plant distribution within two polar desert landscapes. *Arctic and Alpine Research* **26**, 46–55.
- BOSLOUGH, M. B. (1991). Shock modification and chemistry and planetary geologic processes. *Annu. Rev. Earth Planet. Sci.* 1991 **19**, 101–130.
- BOUCHARD, M. A. (ed.) (1989). *L'histoire naturelle du Cratère du Nouveau-Québec*. Collection Environment et géologie, 7. Département de géologie, Université de Montréal.
- BOUCHARD, M. A. & SAARNISTO, M. (1989). Déglaciation et paléodrainages du cratère du Nouveau-Québec. Collection Environment et géologie, 7. Département de géologie, Université de Montréal.
- BURBA, G. G. (1997). Astroblemes: unique terrestrial ecosystems. *Meteoritics and Planetary Science* (Abstract) **32**, A24.
- CABROL, N. A. & GRIN, E. A. (1995). A morphological view on potential niches for exobiology on Mars. *Planet. Space Sci.* **43**, 179–188.
- CABROL, N. A., GRIN, E. A. & DAWIDOWICZ, G. (1996). Ma'adim Vallis revisited through new topographic data: evidence for an ancient intravalley lake. *Icarus* **123**, 269–283.
- CASSIDY, W. A. (1954). The Wolf Creek, Western Australia, meteorite crater. *Meteoritics and Planetary Sciences* **1**, 197–199.
- CASSIDY, W. A. & RENARD, M. L. (1996). Discovering research value in the Campo del Cielo Argentina, meteorite craters. *Meteoritics and Planetary Sciences* **31**, 433–448.
- CHAPIN, F. S. (1980). Mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* **11**, 233–260.
- CHYBA, C. F., THOMAS, P. J., BROOKSHAW, L. & SAGAN, C. (1990). Cometary delivery of organics molecules to the early earth. *Science* **249**, 366–373.
- CLARKE, B. C. (1988). Primeval pro-creative comet pond. *Origins of Life Evol. Biosphere* **18**, 209–238.
- CLASSEN, J. (1978). The meteorite craters of Morasko in Poland. *Meteoritics and Planetary Sciences* **13**, 245–255.
- COCKELL, C. S. & STOKES, D. M. (1999). Polar winter: a biological model for impact events and related dark/cold climatic changes. *Climatic Change* **41**, 151–173.
- COCKELL, C. S., BRANDT, D., HAND, K., & LEE, P. (2001a) Microbial mats in the Tswaing impact crater. Results of a South African exobiology expedition and implications for the search for biological molecules on Mars. *Lunar and Planet. Sci. Conf.* (32nd). Abstract.
- COCKELL, C. S., LEE, P., HILDALGO, L., SCHUERGER, A., STOKES, D. & JONES, J. (2001b). Microbiology and vegetation of micro-oases and polar desert, Haughton Impact Crater, Devon Island, Nunavut, Canada. *Arctic, Alpine and Antarctic Research* **33**, 306–318.
- DEHM, R., GALL, H., HOEFLING, R., JUNG, W. & MALZ, H. (1977). Animal and plant remains from the Upper Miocene Ries Lake. *Geologica Bavarica* **75**, 91–110.
- DELISLE, C. E., BOUCHARD, M. A. & ANDRE, P. (1986). Les précipitations acides et leurs effets potentiels au nord du 55° parallèle du Québec. Collection Environment et géologie, 7. Département de géologie, Université de Montréal.
- DEL MORAL, R. & WOOD, D. M. (1988). Dynamics of herbaceous vegetation recovery on Mount St. Helens, Washington, USA, after a volcanic eruption. *Vegetatio* **74**, 11–27.

- DEL MORAL, R. & WOOD, D. M. (1993). Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. *Amer. J. Bot.* **80**, 981–991.
- DENCE, M. R. (1972). The nature and significance of terrestrial impact structures. *XXIV International Geological Congress Proceedings*, Section **15**, 77–89.
- DYMOND, J., COLLIER, R. W. & WATMOOD, M. E. (1989). Bacterial mats from Crater-lake, Oregon, USA and their relationship to possible deep-lake hydrothermal venting. *Nature* **342**, 673–675.
- EMRICH, G. H. & BERGSTROM, R. E. (1962). Des Plaines disturbance, Northeast Illinois. *Geological Society of America Bulletin* **73**, 959–968.
- ENGLUND, K. J. & ROEN, J. B. (1962). Origins of the Middleboro Basin, Kentucky. *US Geological Survey Professional Paper* **450E**, 20–22.
- FARMER, J. D. (1995). Mars exopalaeontology. *Palaios* **10**, 197–198.
- FREDRIKSSON, K., DUBE, A., MILTON, D. J. & BALASUNDARAM, M. (1973). Lonar Lake, India: an impact crater in basalt. *Science* **180**, 862–864.
- FRISCH, T. & THORSTEINSSON, R. (1978). Haughton astrobleme: a mid-cenozoic impact crater Devon Island, Canadian Arctic Archipelago. *Arctic* **31**, 108–124.
- FUDALI, R. F. (1973). Roter Kamm: evidence for an impact origin. *Meteoritics and Planetary Sciences* **8**, 245–257.
- GLASSTONE, S. & DOLAN, P. J. (1977). The Effects of Nuclear Weapons. United States Department of Defense and the United States Department of Energy, Washington, DC.
- GORTHNER, A. (1992). Morphology, function and evolution of complex gastropod shells in long-lived lakes with a contribution to the paleobiology of *Gyraulus multiformis* in the Steinheim basin. *Stuttgarter Beitrage zur naturkunde serie B (Geologie und palaeontologie)* **190**, 1–173.
- GREEN, J., MOGHRABY, A. I. & ALI, O. M. M. (1979). Biological observations on the crater-lakes of Jebel Marra, Sudan. *Journal of Zoology* **189**, 493–502.
- GRIEVE, R. A. F. (1988). The Haughton impact structure: summary and synthesis of the results of the HISS project. *Meteoritics and Planetary Sciences* **23**, 249–254.
- GRIEVE, R. A. F. & MASAITIS, V. L. (1994). The economic potential of terrestrial impact craters. *Int. Geol. Rev.* **36**, 105–151.
- GRONLUND, T., LORTIE, G., GUILBAULT, J. P., BOUCHARD, M. A. & SAANISTO, M. (1990). Diatoms and arcellaceans from Lac du Cratere du Nouveau-Quebec, Ungava, Quebec, Canada. *Canadian J. Botany* **68**, 1187–1200.
- GUROV, E. P. (1996). The Boltysh impact crater: Lake Basin with a heated bottom. (Abstract). International Workshop, Tunguska 96. Bologna, Italy.
- HALL, J. B., SWAINE, M. D. & TALBOT, M. R. (1978). An early Holocene leaf flora from Lake Bosumtwi, Ghana. *Palaeogeography, Palaeoclimatology, Palaeoecology* **24**, 247–262.
- HARTUNG, J. B. & ANDERSON, R. R. (1988). A compilation of information and data on the Manson impact structure. LPI Tech Report 88–08. Lunar and Planetary Institute, Houston, 32 pp.
- HENRY, G. H. R., FREEDMAN, B. & SVOBODA, J. (1986). Effects of fertilization on three tundra plant communities at a polar desert oasis. *Canadian J. Botany* **64**, 2502–2507.
- HICKEY, L. J., JOHNSON, K. R. & DAWSON, M. R. (1988). The stratigraphy, sedimentology, and fossils of the Haughton formation: a post-impact crater-fill, Devon Island, N.W.T., Canada. *Meteoritics and Planetary Sciences* **23**, 221–231.
- HILDEBRAND, A. R., PENFIELD, G. T., KRING, D. A., PILKINGTON, M., CAMARGO, A., JACOBSEN, S. B. & BOYNTON, W. V. (1991). Chicxulub crater – a possible Cretaceous Tertiary boundary impact crater on the Yucatan Peninsula, Mexico. *Geology* **19**, 867–871.
- HOEFELING, R., HOEFS, J., HOLLERBACH, A. & HUFNAGEL, H. (1977). Tertiary lake sediments of Reis research bore hole, Noerdlingen, West Germany, 1973. A summary. *Geologica Bavarica* **75**, 13–20.
- HODGE, P. (1994). Meteorite craters and impact structures of the Earth. Cambridge Univ. Press, 124 pp.
- JANSA, L. F. (1993). Cometary impacts into ocean: their recognition and the threshold constraint for biological extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* **104**, 271–286.
- JANSA, L. F. & PE-PIPER, G. (1987). Identification of an underwater extraterrestrial impact crater. *Nature* **327**, 612–614.
- KARL, D. M., BRITAIN, A. M. & TILBROOK, B. D. (1989). Hydrothermal and microbial processes at Loihi Seamount (Hawaii, USA), a mid-plate hot-spot volcano. *Deep Sea Research. Part A: Oceanographic Research Papers* **36**, 1655–1674.
- KIZITO, Y. S., NAUWERCK, A., CHAPMAN, L. J. & KOSTE, W. (1993). A limnological survey of some western Uganda crater-lakes. *Limnologia* **23**, 335–347.
- KOEBERL, C., FREDRIKSSON, K., GOTZINGER, M. & REIMOLD, W. U. (1989). Anomalous quartz from the Roter Kamm impact crater, Namibia: evidence for post-impact hydrothermal activity. *Geochim. Cosmochim. Acta* **53**, 2113–2118.
- KOLESNIKOVA, N. V., KOLESNIKOV, E. M., BOTTGER, T. & JUNGE, F. (1996). Isotopic anomaly in peat nitrogen – a probable trace of acid rain caused by the Tunguska bolide in 1908. (Abstract). International Workshop, Tunguska 96. Bologna, Italy.
- KRING, D. A. (1997). Air blast produced by the Meteor Crater impact event and a reconstruction of the affected environment. *Meteoritics and Planetary Science* **32**, 517–530.
- LEE, P. (1993). Briny lakes on early Mars? Terrestrial intracrater playas and martian candidates. *LPI Tech. Rep. 93-03, Part 1*, 17.
- LEE, P., BUNCH, T. E., CABROL, N., COCKELL, C. S., GRIEVE, R. A. F., MCKAY, C. P., RICE, J. W. JR., SCHUTT, J. W. & ZENT, A. P. (1998). Haughton-Mars 97 – I: Overview of observations at the Haughton impact crater, a unique Mars analog site in the Canadian High Arctic. Lunar Planet Sci. Conf. XXIX, 1973–1974.
- LONG, M. (1999). Mars on Earth. National Geographic Magazine, July, 34–51. National Geographic Society, Washington DC.
- LONGO, G., GALLI, M. & SERRA, R. (1996). The testimony of the surviving Tunguska trees. (Abstract). International Workshop, Tunguska 96. Bologna, Italy.
- LOZEJ, G. P. & BEALS, F. W. (1975). The unmetamorphosed sedimentary fill of the Brent meteorite crater, Southern-eastern Ontario. *Can. Journ. Earth Sci.* **12**, 606–628.
- MALLORY, F. F. & BOOTS, B. N. (1983). Spatial distribution of lemming mats in the Canadian high arctic. *Revue Canadienne de Zoologie* **61**, 99–107.
- MALTAIS, M. J. & VINCENT, W. F. (1997). Periphyton community structure and dynamics in a subarctic lake. *Canadian Journal of Botany* **75**, 1556–1569.

- MCKAY, C. P. & DAVIS, W. L. (1991). The duration of liquid water habitats on Mars. *Icarus* **90**, 214–221.
- MELOSH, H. J. (1989). Impact cratering. A geologic process. Oxford Univ. Press, 245 pp.
- MUC, M., FREEDMAN, B. & SVOBODA, J. (1989). Vascular plant communities of a polar oasis at Alexandra Fiord (79°N), Ellesmere Island, Canada. *Canadian J. Botany* **67**, 1126–1136.
- NEWSOM, H. E., GRAUP, G., SEWARDS, T. & KEIL, K. (1986). Fluidization and hydrothermal alteration of the suevite deposit at the Ries crater, West Germany, and implications for Mars. *J. Geophys. Res.* **91**, E239–E251.
- NEWSOM, H. E., BRITTELLE, G. E., HIBBITTS, C. A., CROSSEY, L. J. & KUDO, A. M. (1996). Impact crater-lakes on Mars. *J. Geophys. Res.* **101**, 14,951–14,955.
- NOLD, S. C. & WARD, D. M. (1995). Diverse *Thermus* species inhabit a single hot-spring microbial mat. *Systematic and Applied Microbiology* **18** (2), 274–278.
- OMAR, G., JOHNSON, K. R., HICKEY, L. J., ROBERTSON, P. B., DAWSON, M. R. & BARNOSKY, C. W. (1987). Fission-track dating of Haughton Astrobleme and included biota, Devon Island, Canada. *Science* **237**, 1603–1605.
- ONER, M. & OFLAS, S. (1977). Plant succession on the Kula Volcano in Turkey. *Vegetatio* **34**, 55–62.
- OSINSKI, G. R., SPRAY, J. G. & LEE, P. (2001). Impact-induced hydrothermal activity within the Haughton impact structure, arctic Canada: generation of a transient, warm, wet oasis. *Meteoritics and Planetary Sciences* **36**, 731–745.
- PARTRIDGE, T. C. (1999). Tswaing. Investigations into the origin, age and paleoenvironments of The Pretoria Saltpan. Council for Geoscience. Geological Survey of South Africa. Memoir 85, Pretoria. 198 pp.
- PARTRIDGE, T. C., KERR, S. J., METCALFE, S. E., SCOTT, L., TALMA, A. S. & VOGEL, J. C. (1993). The Pretoria saltpan. A 200,000 year southern african lacustrine sequence. *Palaeogeography, Palaeoclimatology, Palaeoecology* **101**, 317–337.
- POHL, J., STOFFLER, D., GALL, H. & ERNSTON, K. (1977). The Ries impact crater. In Impact and explosion cratering (eds D. J. Roddy, R. O. Pepin and R. B. Merrill). Permagon, New York. pp. 343–404.
- POHL, J., ECKSTALLER, A. & ROBERTSON, P. B. (1988). Gravity and magnetic investigations in the Haughton impact structure, Devon Island, Canada. *Meteoritics and Planetary Sciences* **23**, 235–238.
- PRIEUR, D., ERAUSO, G. & JEANTHON, C. (1995). Hyperthermophilic life at deep-sea hydrothermal vents. *Planetary and Space Science* **43** (1–2), 115–122.
- RAMPINO, M. R., SELF, S. & STOTHERS, R. B. (1988). Volcanic winters. *Annual Reviews of Earth and Planetary Sciences* **16**, 73–99.
- REDEKER, H.-J. & STOFFLER, D. (1988). The allochthonous polymict breccia layer of the Haughton impact crater, Devon Island, Canada. *Meteoritics* **23**, 185–196.
- REEVES, F. & CHALMERS, R. O. (1949). The Wolf Creek crater. *Austral. J. Sci.* **11**, 154–156.
- REIF, W. E. (1983). The Steinheim snails (Miocene, Schwabian Albian) from a neo-Darwinism point of view: a discussion. *Palaeontologische Zeitschrift* **57**, 21–26.
- REIMOLD, W. U., BARNDT, D., DE JONG, R., HANCOX. (1999) The Tswaing Meteorite Crater. Council for Geoscience, Geological Survey of South Africa. pp. 171.
- REYNOLDS, R. T., MCKAY, C. P. & KASTING, J. F. (1987). Europa, tidally heated oceans, and habitable zones around giant planets. *Adv. Space. Res.* **7**, 125–132.
- RICHARD, P. J. H., BOUCHARD, M. A. & GANGLOFF, P. (1991). The significance of pollen-rich inorganic lake sediments in the Cratère du Nouveau-Quebec area, Ungava, Canada. *Boreas* **20**, 135–150.
- RIDING, R. (1979). Origin and diagenesis of lacustrine algal bioherms at the margin of the Ries crater, Upper Miocene, Southern Germany. *Sedimentology* **26**, 645–680.
- ROBBINS, E. I. & IBERALL, A. S. (1991). Mineral remains of early life on earth? On Mars? *Geomicrobiology Journal* **9**, 51–66.
- ROBERTSON, P. B. & GRIEVE, R. A. F. (1975). Impact structures in Canada: their recognition and characteristics. *Journal of the Royal Astronomical Society of Canada* **69**, 1–20.
- ROBERTSON, P. B. & MASON, G. D. (1975). Shatter cones from Haughton Dome, Devon Island, Canada. *Nature* **255**, 393–394.
- ROBERTSON, P. B. & SWEENEY, J. F. (1983). Haughton impact structure: structural and morphological aspects. *Can. Journ. Earth Sci.* **20**, 1134–1151.
- ROBERTSON, P. B., OSTERTAG, R., BISCHOFF, L., OSKIERSKI, W., HICKEY, L. J. & DAWSON, M. R. (1986) First results of a multidisciplinary analysis of the Haughton impact crater, Devon Island, Canada *Lunar Planet. Sci.* **16**, 702.
- ROSENBERG, R. (1976). Benthic faunal dynamics during succession following pollution abatement in a swedish estuary. *Oikos* **27**, 414–427.
- RUFF, S. W. (2000). “White Rock” lacks evidence of an aqueous origin: the search for martian evaporates continues. *Astrobiology Conference, NASA Ames Research Center* (Abstract).
- SAARSE, L., RAJAMAE, R., HEINSALU, A. & VASSILVEJ, J. (1991). The biostratigraphy of sediments deposited in the Lake Kaali meteorite impact structure, Saaremaa Island, Estonia. *Bulletin of the Geological Society of Finland* **63**, 129–139.
- SALONEN, V. P., ERIKSSON, B. & GRONLUND, T. (1992). Pleistocene stratigraphy in the Lappajarvi meteorite crater in Ostrobothnia, Finland. *Boreas* **21**, 253–269.
- SANCHEZ, J. & CASSIDY, W. A. (1966). A previously undescribed crater in Chile. *J. Geophys. Res.* **71**, 4891–4895.
- SCHOEMAN, F. R. & ASHTON, P. J. (1982). The diatom flora of the Pretoria Salt Pan, Transvaal, Republic of South Africa. *Bacillaria* **5**, 63–99.
- SCHONHEIT, P. & SCHAFER, T. (1995). Metabolism of hyperthermophiles. *World Journal of Microbiology and Biotechnology* **11** (1), 26–57.
- SCHULTEN, R. B. (1975). Some flowering plants of the Devon island lowlands. *Arctic* **28**, 93–98.
- SCHULTZ, P. H. & LIANZA, R. E. (1992). Recent grazing impacts on the earth: the Rio Cuarto crater field, Argentina. *Nature* **355**, 234–237.
- SCHWEIGERT, G. (1993). The middle miocene flora (MN7) of Steinheim am Albuch (Swabian Jura, Baden-Wuerttemberg). *Jahreshefte der Gesellschaft fuer Naturkunde in Wuerttemberg* **148**, 61–96.
- SCOTT, D. H., RICE, J. W. & DOHM, J. M. (1991). Martian paleolakes and waterways: exobiological implications. *Origins Life Evol. Biosph* **21**, 189–198.
- SEGERER, A. H., BURGGRAF, S., FIALA, G., HUBER, G., HUBER, R., PLEY, U. & STETTER, K. O. (1993). Life in hot springs and hydrothermal vents. *Origins Life Evol. Biosphere* **23**, 77–90.
- SHIRO, T. & ROGER, M. (1995). Species attributes in early primary succession on volcanoes. *Journal of Veg. Sci.* **6**, 517–522.
- SHOEMAKER, E. & SHOEMAKER, C. (1988). Impact structures of Australia. *Lunar and Planetary Science* **19**, 1079–1080.

- SKOPETS, M. (1992). Secrets of Siberia's white lake *Nat. Hist.*, Nov 1992, 2–4.
- SLEEP, N. H., ZAHNLE, K. J., KASTING, J. F. & MOROWITZ, H. J. (1989). Annihilation of ecosystems by large asteroidal impacts on the early earth. *Nature* **342**, 139–142.
- SMITH, D. (1996). *The Meteor Crater Story*. Meteor Crater Enterprises, Inc. 79 pp.
- SOUTHERN, W., ASH, J., BRODIE, J. & RYAN, P. (1986). The flora, fauna and water chemistry of Tagimaucia crater, a tropical highland lake and swamp in Fiji (Pacific Ocean). *Freshwater Biology* **16**, 509–520.
- SUBBARAO, K. V. (1999). Deccan Volcanic Province: Geomorphology, mineralogy and petrology. Bangalore, 398pp.
- SVOBODA, J. & FREEDMAN, B. (1981). Ecology of a high arctic lowland oasis Alexandra Fiord (78° 53' N, 75° 55' W), Ellesmere Island, NWT, Canada. University of Toronto, Department of Botany, Toronto, Canada.
- TAGAWA, H., SUZUKI, T., PARTOMIHARDJO, T. & SURIADARMA, A. (1985). Vegetation and succession on the Krakatau islands, Indonesia. *Vegetatio* **60**, 131–145.
- THOMAS, V. G. & MACDONALD, S. D. (1985). The significance of terrestrial and marine oases in the high arctic. In *Proceedings of the Arctic Heritage Symposium*, Banff, Alberta, ed., J. G. Nelson, R. Needham and L. Norton. Canadian Park Services, pp. 147–153.
- THOMPSON, W. R. & C. SAGAN (1992). Organic chemistry on Titan–Surface Interactions. In *Proc. ESA Symp. on Titan*. ESA SP-338, 167–176.
- THORNTON, I. W. B. (1984). Psocoptera of the Hawaiian islands, Part III. The endemic *Ptycta* complex (Psocidae): systematics, distribution and evolution. *International Journal of Entomology* **26**, 1–128.
- THORNTON, I. W. B., NEW, T. B., ZANN, R. A. & RAWLINSON, P. A. (1990). Colonization of the Krakatau islands by animals: a perspective from the 1980's. *Proceedings of the Royal Society of London* **328**, 131–165.
- TODD, B. J. (1978). Gravity study of the Haughton Dome, Devon Island, Northwest Territories. B.Sc Thesis, University of Western Ontario, 68 pp.
- TOON, O. W., ZAHNLE, K., MORRISON, D., TURCO, R. P. & COVEY, C. (1997). Environmental perturbations caused by the impacts of asteroids and comets. *Reviews of Geophysics* **35**, 41–78.
- TURCO, R. P., TOON, O. B., PARK, C., WHITTEN, R. C., POLLACK, J. B. & NOERDLINGER, P. (1982). An analysis of the physical, chemical, optical and historical impacts of the 1908 Tunguska meteor fall. *Icarus* **50**, 1–52.
- TURNER, B. F., GARDNER, L. R., SHARP, W. E. & BLOOD, E. R. (1996). The geochemistry of Lake Bosumtwi, a hydrologically closed basin in the humid zone of tropical Ghana. *Limnol. Oceanog* **41**, 1415–1424.
- UHE, G. (1988). The composition of the plant communities inhabiting the recent volcanic deposits of Maui and Hawaii, Hawaiian islands. *Trop. Ecol.* **29**, 26–47.
- UPFIELD, A. (1934). reprinted in 1947. *Death of a swagman*. Doubleday, Doran and Co. Ltd, Garden City, New York. pp. 221.
- UUTELA, A. (1990). Proterozoic microfossils from the sedimentary rocks of the Lappajarvi impact crater (Finland). *Bulletin of the Geological Society of Finland* **62**, 115–120.
- VESTER, H. F. M. & CLEEF, A. M. (1998). Tree architecture and secondary tropical rain forest development: a case study in Araracuara, Colombian Amazonia. *Flora* **193**, 75–97.
- WALKER, B. D. & PETERS, T. W. (1977). Soils of the Truelove lowland and plateau. In L. C. Bliss (ed.) *Truelove Lowland, Devon Island, Canada: A high arctic ecosystem*. Edmonton: University of Alberta Press, 31–62.
- WALTER, M. R. (1996). Ancient hydrothermal ecosystems on earth: a new paleobiological frontier. *CIBA Foundation Symposia* **202**, 112–130.
- WARD, A. W. (1979). Yardangs on Mars: Evidence for recent wind erosion, *J. Geophys. Res.* **84**, 8147–8166.
- WARD, A. K., BAROSS, J. A., DAHM, C. N., LILLEY, M. D. & SEDELL, J. R. (1983). Qualitative and quantitative observations on aquatic algal communities and recolonization within the blast zone of Mount St. Helens 1980 and 1981. *Journal of Phycology* **19**, 238–247.
- WHITLOCK, C. & DAWSON, M. R. (1990). Pollen and vertebrates of the early Neogene Haughton Formation, Devon Island, Arctic Canada. *Arctic* **43**, 324–330.
- WILLIAMS, G. E. (1994). Acraman, South Australia: Australia's largest meteorite impact structure. *Proceedings of the Royal Society of Victoria* **106**, 105–127.
- WOOD, D. M. & MORRIS, W. F. (1990). Ecological constraints to seedling establishment on the Pumice Plains, Mount St. Helens, *Washington. Amer. J. Bot.* **77**, 1411–1418.
- ZAHNLE, K. (1990). Atmospheric chemistry by large impacts. In *Global catastrophes in earth history*. eds. V. Sharpton and P. Ward. *Spec. Pap. Geol. Soc. Am.* **247**, 271–288.