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# Microscale biopitting by the endolithic lichen *Verrucaria baldensis* and its proposed role in mesoscale solution basin development on limestone

John P. McIlroy de la Rosa,\* Patricia A. Warke and Bernard J. Smith

School of Geography, Archaeology and Palaeoecology, Queen's University Belfast, Belfast, UK

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\*Correspondence to: John P. McIlroy de la Rosa, School of Geography, Archaeology and Palaeoecology, Queen's University Belfast, Belfast BT7 1NN, UK. E-mail: jmcilroydelarosa01@qub.ac.uk

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**ABSTRACT:** Data are reported demonstrating the potential role of microscale morphologies, induced by endolithic lichen communities, specifically *Verrucaria baldensis*, in the initiation and development of mesoscale solution basin formation on limestone in the Burren, County Clare. A biophysical model is proposed outlining the different microscale stages leading to solution basin initiation with a progression from initial lichen colonization and growth, associated perithecial biopitting followed by biopit coalescence to form biotroughs, their subsequent enlargement and eventual incipient solution basin formation. This model provides one explanation for solution basin development as this end state may also be achieved through simple solutional means without biological input. The complexity of interactions at the lichen–rock interface are identified with emphasis on the spatial and temporal variability of these underlining the point that, as with macrotopographies at the landscape scale, rock surface microtopographies also reflect historical weathering legacies. Copyright © 2011 John Wiley & Sons, Ltd.

**KEYWORDS:** limestone; lichen; biopitting; biotroughs; *Verrucaria (Bagliettoa) baldensis*; weathering; karst

## Introduction

Identifying the links between morphological features at different scales is of increasing importance to the geomorphological community, as a better understanding of these links is seen as key to comprehending the initiation of many mesoscale weathering forms through the action of processes operating at the nanoscale and microscale (Viles, 2001).

The processes by which lichens alter stone surfaces have long been of interest to geologists and geomorphologists (e.g. Geikie, 1893; Fry, 1922). However, the contribution of lichen-induced nanoscale and microscale weathering morphologies to the development of mesoscale weathering landforms in karst environments, where calcicolous lichen communities often provide extensive cover, is relatively understudied. Furthermore, the association between lichens and rock weathering *per se* is not a simple one with a growing body of evidence that questions the traditional assumptions of lichen as agents of bio-deterioration, linking some species with active and passive bio-protection of rock surfaces (Ariño *et al.*, 1995; Viles, 1995; Fiol *et al.*, 1996; Mottershead and Lucas, 2000; Carter and Viles, 2003, 2004, 2005; Portero de la Torre *et al.*, 2004).

Spatial variation in surface alteration induced by different species of lichen reflects the innate complexity of these life forms and highlights the need for better understanding of their life cycles, the nature of their interaction with rock and the

significance of their long-term contribution to the weathering system. In particular, much remains to be learned of the wider geomorphological significance of lichen to the development of larger-scale limestone weathering features as only a few studies have sought to demonstrate links across these scale boundaries. For example, Fiol *et al.* (1996) show how micro-morphologies associated with free-living algae contribute to mesoscale rillenkarren formation in Mallorca, while Viles (1995) suggests that microscale biopits created by endolithic lichen fruiting bodies on rock surfaces may be subsequently enlarged by dissolution following lichen death.

Microscale morphologies such as biopits are frequently reported on limestone with certain endolithic species noted for their production of well-rounded pits (c. 0.2–1.5 mm in diameter), deeply immersed in their substratum and exposed following ascospore dispersal (Fry, 1922; Danin *et al.*, 1983; Gehrmann *et al.*, 1992; Danin, 1993). However, despite the frequency of their occurrence on limestone, many gaps exist in our understanding of the wider geomorphological significance of ascomata-induced biopits with the following research question providing the focus for this work:

- Can intensive microscale biopitting by endolithic lichen communities contribute to the initiation and development of mesoscale karren features, specifically solution basins on limestone?

The following section provides a brief overview of the key characteristics of endolithic lichens including their environmental preferences and reproductive strategies, an understanding of which is essential for interpreting the rock surface micromorphologies associated with them.

## Endolithic lichens, fruiting bodies and biopitting

Lichens are stable, self-supporting associations of a mycobiont (fungus) and a photobiont (algae and/or cyanobacteria) (Hawksworth, 1988) which form a heterogenous structure known as a thallus. Lichens are classified according to their growth form with members of the crustose species, which closely adhere to their substrate, being the slowest growing. Radial growth rates of crustose species vary with the favourability of environmental conditions, but are usually between 0.5 and 2.0 mm per year (Hale, 1973).

The crustose morphological group can be sub-divided into epilithic and endolithic species, often distinguished by whether they exist on the rock surface or within the substrate. However, many lichen species commonly described as epilithic, have an endolithic component as their hyphae penetrate pores, cracks and crevices in order to anchor themselves. Similarly, endolithic species, largely inhabiting the rock matrix, generally have an epilithic component with fruiting bodies commonly exposed at the rock surface. Consequently, a more accurate distinction is made on the basis of the location of the photobiont in relation to the rock substrate. In epilithic species, the photosynthetic tissue is primarily on the rock surface, while in endolithic species it is located within the mineral lattice of the rock substrate.

The depth to which the endolithic lichen hyphae can penetrate the rock substrate is determined by thallus age, substrate properties (mineralogy, porosity, microfissures, etc.) and substrate light transmissivity (Hall *et al.*, 2008), as the photobiont requires solar radiation to photosynthesize. Endolithic lichens are common in temperate regions but their diversity is reduced in comparison to epilithic species, with only 7.4% of calcicolous crustose lichens in Western Europe classified as endolithic (Tretiach, 1995).

Endolithic varieties can be further subdivided into cryptoendolithic forms occupying structural cavities, chasmoendolithic forms which inhabit fissures and cracks, and euendolithic forms which actively bore into rocks by dissolving their substratum (Chen *et al.*, 2000) with the latter group generally being restricted to calcareous materials (Bungartz *et al.*, 2004). It is this latter group that forms the focus of this paper.

Lichens reproduce by forming fruiting bodies known as ascospores, which provide the means for the formation and release of spores. In the case of crustose lichens, ascospores are differentiated into perithecia and apothecia based on slight differences in their morphology, although they fulfil the same function of ascospore formation and dispersal. The significance of these features is that sub-microscale pits, referred to as biopits, are left on rock surfaces when the apothecia or perithecia of endolithic lichens fulfil their reproductive role and decay.

Throughout this paper and in line with other researchers (e.g. Viles, 1995; Bungartz *et al.*, 2004), the terms 'biopit' or just 'pit' are used to describe these microscale features, although within the literature they are also referred to as mesopits (Mohammadi, 2008; Favero-Longo *et al.*, 2009) and internal mesopits (Khodosovtsev, 1995). In addition to a lack of commonality over terminology, discrepancies also exist within the literature when it comes to defining spatial scales of analysis and weathering features. Definition of the size categories referred to in this paper is shown in Table I.

## Field Site Description

Located in the north of County Clare, western Ireland, the Burren (Figure 1) constitutes an area of approximately 250 km<sup>2</sup> with 15 km<sup>2</sup> designated as a National Park. The Burren is characterized by temperate maritime climatic conditions with a mean annual rainfall of 1600 mm and an average annual temperature of 10.1 °C, ranging from 5.4 °C in January to 15.7 °C in July (Met Éireann, 2010).

Geologically, the Burren is composed primarily of Lower Carboniferous limestone and was subject to Pleistocene glaciations evident in the existence of south-westerly orientated glacial striae (Mitchell, 1981), scoured, often stepped hills (Figure 2a), drumlin-like formations, and extensive areas of bare limestone pavements (Figure 2b) (Moles and Moles, 2002). The glacio-karstic landscape of the Burren is a product of solution processes throughout the last 10,000 years and comprises a hierarchy of surface forms (see Table I).

Macroscale examples include poljes, such as the Carran depression (Figure 2c), which is 60 m in depth and covers an area of c. 5 km<sup>2</sup>. Large solution features such as collapsed dolines, which form more moderately sized depressions, are also found in abundance throughout the Burren. There are also numerous turloughs, such as Carran Turlough (Figure 2c), which are seasonally dry groundwater-fed lakes, formed in glacially excavated or solutional hollows in the limestone.

Developed upon these macroscale features are mesoscale weathering forms, with solutional features such as kamenitzes (Figure 2d), rinnenkarren (Figure 2e) and meanderkarren (Figure 2f) being some of the most common mesomorphologies associated with limestone pavements. Finally, superimposed upon these mesoscale features are the micromorphologies (biopits and biotroughs) that form the focus of this paper.

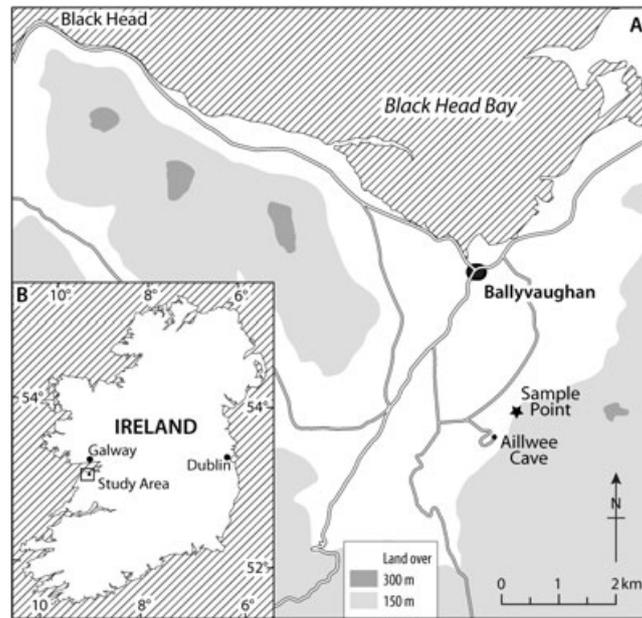
## Materials and Methods

### Sample location and description

Samples were collected from limestone exposed on a gently sloping, stepped, north-westerly facing hill approximately 3.5 km from Galway Bay and 500 m northeast from the entrance to Aillwee cave (Figure 1). The location is approximately

**Table I.** Spatial scales and associated features referred to in this paper

Scale description	Size range	Feature	Viewing technique
Nano	<250 µm	Calcite crystal etching/crystal boundary widening	Electron microscope
Sub-micro	0.25–2 mm	Perithecial biopits	Light/stereo microscope
Micro	2–20 mm	Biotroughs (networks of coalesced biopits)	Light/stereo microscope
Sub-meso	2–50 cm	Embryonic solution basin	Human eye/hand specimen
Meso	50 cm–2 m	Mature solution basin	Human eye/hand specimen
Macro	>2 m	Limestone pavement	Human eye/aerial photograph



**Figure 1.** Geographical setting of the sample location within the Burren, Co. Clare, Republic of Ireland.



**Figure 2.** Karst geomorphology at a variety of scales, the Burren, Co. Clare. (a) Gently dipping, terraced limestone strata near Kilnaboy. (b) Limestone pavement with characteristic clints (flackkarren) and grikes (kluftkarren). (c) Carran Turlough within the Carran depression/polje. (d) Solution basins (kamenitza) 10–20 cm in diameter on limestone pavement at Poul nabrone. (e) Solution runnels (rinnenkarren) on an inclined section of limestone pavement at Poul sallah. (f) Meanderkarren approximately 1 m long channelling overflow from a solution basin at Poul sallah.

150 m above sea level (a.s.l.) and corresponds to the lower Aillwee Member of the Burren Limestone Formation from the Viséan age (Sleeman *et al.*, 2008). The local lithotype is described as a bedded and massive, pale grey, occasionally fossiliferous limestone (Sleeman *et al.*, 2008).

The study area is characterized by slightly inclined limestone pavements on which surface karren features such as kamenitze and meanderkarren are abundant and well developed. Lichen colonization is widespread, with *Verrucaria baldensis* (Figure 3) being especially abundant with relict and active perithecial biopits on rock surfaces indicating the activity of past and present endolithic lichen communities.

Thin-section analysis of samples (Figure 4) identified a predominantly crystalline calcite mineralogy with subordinate nodular chert and micritic or sparry calcite. Larger crystalline calcite grains exhibit good cleavage and are typically set within a mosaic of smaller calcite crystals. Limestone porosity is mainly comprised of intergranular joints and intragranular microfractures with evidence of calcite crystal corrosion observed at high magnification.

A cross-section of the rock surface and subsurface shows obvious weathering with fine crystalline calcite forming an undulating biotrough morphology. Intragranular porosity is high at the lichen–rock interface with small calcite crystals visible within thalline areas as a consequence of hyphal penetration. An outer black coating appearing to be organic material is present within biotroughs.

### Sample preparation and analysis

The samples collected represent the variety of lichens, their coverage and the local limestone surface micromorphologies. Samples were characterized by visibly biopitted surfaces, with

extensive coverage of mature endolithic lichens exhibiting apothecia and perithecia. Photographs were taken *in situ* of successively biopitted areas and solution basins at various stages of development, as it was not feasible to remove large slabs of rock from the study area. Samples were analysed under an Olympus S2X12 binocular stereomicroscope with zoom magnification up to  $\times 90$ . Images were captured digitally using a Moticam 5000. The following endolithic species (Table II) were observed *in situ* at the sample location and subsequently identified with more precision in the laboratory by means of chemical tests and ascospore observation.

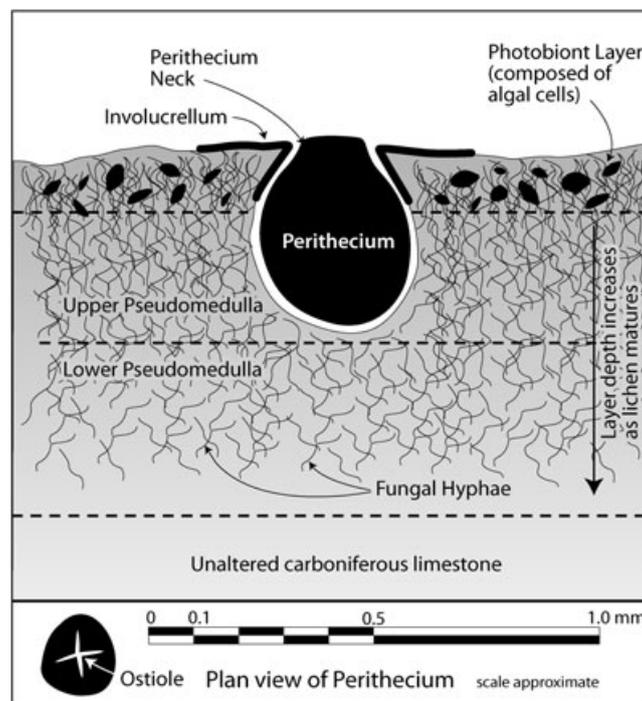
Following surface analysis and in preparation for dry-cutting and thin sectioning to expose cross-sectional surfaces, rock samples were coated in epoxy resin in order to ensure stability of the lichen covered surfaces and the lichen–rock interface.

## Results

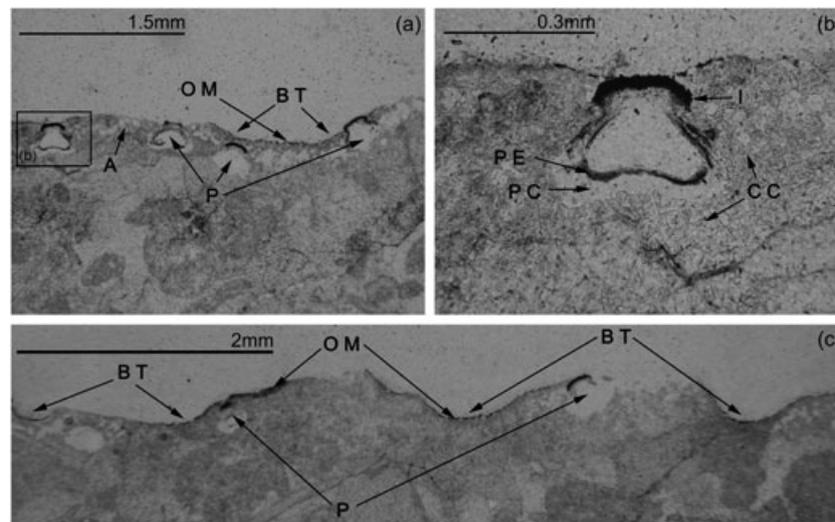
### Characteristics of *Verrucaria baldensis*

The taxonomy of the Verrucariaceae has recently been revised, with *Verrucaria baldensis* being reassigned to the strictly calcicolous and euendolithic *Bagliettoa* genus, and renamed *Bagliettoa baldensis* (A.Massal.) (Gueidan *et al.*, 2009). However, due to the number of previous studies referring to this lichen by its original name, *Verrucaria baldensis* is used throughout this paper.

*Verrucaria baldensis* is a euendolithic lichen with abundant immersed perithecia frequently found on hard calcareous and dolomitic substrates. The key structural components of *V. baldensis* are shown in Figure 3.



**Figure 3.** Diagram showing the main structural components of euendolithic *Verrucaria baldensis* with perithecium (adapted from Tretiach and Geletti, 1997; Pinna *et al.*, 1998; Bungartz *et al.*, 2004; Dobson, 2005). Involucrellum – the external cover of the perithecium. Flat in the case of *Verrucaria baldensis*. Photobiont layer – heteromerous (well-defined) layer just beneath the surface. Composed of clusters of trebouxoid algal cells surrounded by mucilage. Perithecium – flask-shaped fruiting body containing eight-spored ascus within the perithecial cavity. Perithecial Neck – narrow, uppermost part of the perithecium which adjoins to the ostiole. Upper Pseudomedulla – area of intense hyphal penetration through calcite cement. Unlike other endolithic lichens that secrete oxalic acid, e.g. *V. rubrocincta*, calcium oxalates have not been identified in *V. baldensis* colonized calcareous substrates. Lower Pseudomedulla – hyphae of the pseudomedulla becomes less abundant with increasing depth. The extent of hyphal penetration depends on lichen age and the precise mineralogy of the substratum. Unaltered Carboniferous Limestone – unweathered minerals beyond the reach of hyphal penetration. Ostiole (plan view) – apical pore through which ascospore masses are discharged.



**Figure 4.** Petrological thin-section of *Verrucaria baldensis* on Carboniferous limestone. Perithecium (P). Biotrough (BT). Algal cells (A). Organic matter (OM). Perithecial cavity (PC). Fungal hyphae with embedded crystalline calcite (CC). Perithecial envelope (PE). Involucrellum (I). Note in (a) the occurrence of perithecial pits at the boundaries of an existing biotrough, potentially enlarging and expanding that biotrough following the emptying of the perithecial cavities. Note in (b) the existence of a clear contact zone between the perithecial cavity and the network of fungal hyphae with enveloped calcite crystals. The cavity is devoid of calcite most likely as a consequence of crystal corrosion associated with organic acid excretion during perithecium development. Note in (c) the undulating biotrough morphology and the presence of organic matter accumulated within biotroughs, possibly contributing to biotrough enlargement through the development of organic acids.

**Table II.** The attributes of some common endolithic lichen species identified at the sample location.

Species	Ascoma type	Ascoma colour	Approximate diameter
<i>Clauzadea immersa</i>	Apothecia	Black	0.5 mm (500 $\mu$ m)
<i>Verrucaria baldensis</i>	Perithecia	Black	0.2 mm (200 $\mu$ m)
<i>Verrucaria hochstetteri</i>	Perithecia	Black	1.0 mm (1000 $\mu$ m)
<i>Protoblastenia incrustans</i>	Apothecia	Yellow	0.5 mm (500 $\mu$ m)
<i>Verrucaria dufourii</i>	Perithecia	Black	0.5 mm (500 $\mu$ m)
<i>Protoblastenia calva</i>	Apothecia	Orange	1.5 mm (1500 $\mu$ m)
<i>Petractis clausa</i>	Apothecia	White	0.5 mm (500 $\mu$ m)

The hyphae of this endolithic lichen penetrate the limestone substrate by exploiting pre-existing pores, voids, and grain boundaries, or more commonly for euendolithic species, by directly dissolving the calcium carbonates of the calcite cement (Bungartz *et al.*, 2004). Favero-Longo *et al.* (2009) observed hyphal penetration by *Verrucaria baldensis* on limestone to a mean depth of 850  $\mu$ m within the rock matrix and up to 2 mm within cracks and microfissures in the substrate.

Endolithic lichens are renowned for their slow growth with radial growth rates for *Verrucaria baldensis* known only from a laboratory culture where, under optimal conditions, a radial growth rate of 1.8 mm per month was recorded for the first three months of culture (Favero-Longo *et al.*, 2009). However, this figure may be largely unrepresentative of the Burren environment, with actual growth rates likely to be significantly lower given fluctuating seasonal climatic conditions and temperature/water stresses associated with local environmental forcing.

In terms of its biochemical effect upon calcareous substrates, *Verrucaria baldensis* is noted for its low carbon dioxide (CO<sub>2</sub>) exchange rate, exhibiting high respiration rates only following resaturation after severe desiccation (Tretiach and Geletti, 1997). Consequently, the production of carbonic acid, derived from CO<sub>2</sub> produced by respiration in the cells of the lichen thallus, is probably limited for this species, with carbonic

acid-induced dissolution of the calcareous substrate likely to be quite low. Furthermore, unlike other endolithic lichens that secrete the chelating agent oxalic acid, calcium oxalates have not been identified in *V. baldensis* colonized calcareous substrates (Pinna *et al.*, 1998), suggesting that the biomineralization processes induced by this particular lichen species are not nearly as significant as for other documented species.

Whilst studies have shown that the preferred habitat of *Verrucaria baldensis* is characterized by low light levels, high humidity (>80%) and low, stable temperature conditions (6–10 °C) (Tretiach and Geletti, 1997), within Mediterranean environments the lichen is also noted for its desiccation-resistance and ability to survive thallus dehydration (although with reduced photosynthetic and metabolic activity) throughout prolonged summer droughts, a trait that has allowed *V. baldensis* to extend into a wide range of environments. McCarthy (1983) identified *V. baldensis* as being predominant on the clints of limestone pavements in the Burren, but much less common or absent within grikes and runnels. Consequently, for this temperate, maritime environment, *V. baldensis* appears to be more suitably adapted to the drier, warmer conditions of raised surfaces, than the cooler, more humid micro-environmental conditions experienced in surface depressions, within which it typically occurs in Mediterranean regions.

## Interpretation

### Solution basin development model

Until recently, the accepted model of solution basin formation was based on the long-term dissolution of limestone by rainfall-derived standing water with biological factors largely identified as playing a subordinate role, limited to organic acids derived from acid-enriched run-off, lithobiont secretion or the decomposition of organic matter within the basin itself. However, research by Moses and Smith (1993) into surface biomodification by the lichen *Collema auriforme*, showed that the calcite mineral lattice had been weakened as fragments of rock had been plucked from the solution basin surface during thallus

contraction/expansion (associated with wetting and drying cycles) and had become embedded within the fungal hyphae. Moses and Smith (1993) concluded that in conjunction with chemical solution, the process of hyphal contraction and expansion could play a significant role in the formation of karstic features including solution basins.

While previous work (e.g. Cooks and Otto, 1990; Moses and Smith, 1993) has emphasized the influence of a mainly physical mechanism for the development of surface morphology in limestone, this paper examines the potential contribution of microscale biogeochemical weathering morphologies as triggers in the initiation and development of mesoscale solution basins, and explores the significance of this for links between different scales of weathering features. A conceptual model (Figure 5) is proposed, illustrating the potential sequence of events that, although primarily of microscale significance, may have larger scale impacts over longer-term timescales.

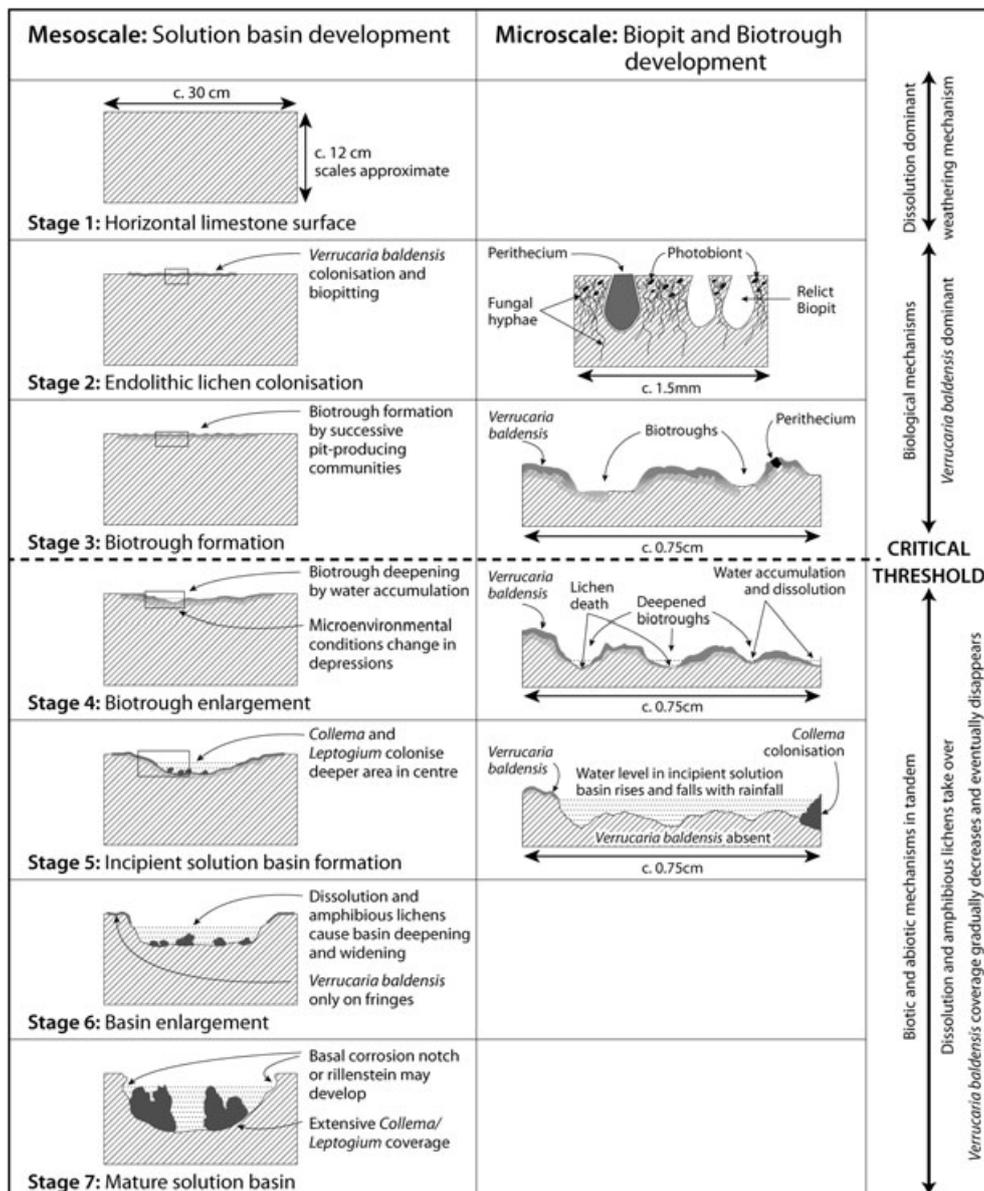
**Stage 1: Horizontal limestone surface**

The model begins with a horizontally bedded or gently sloping limestone surface initially devoid of lichen cover, with

dissolution the dominant weathering mechanism following run-off from precipitation events.

**Stage 2: Endolithic lichen colonization**

The lichen, *Verrucaria baldensis*, colonizes the substrate and begins slow radial growth as hyphae extend themselves vertically and laterally through the weaker calcite cement into the underlying substrate. As the lichen grows it is exposed to periodic rainfall events and water run-off over the surface, however, as the section is slightly inclined, water does not accumulate and is transported as sheet flow into adjacent depressions. The heat retaining capacity of the limestone, which can be up to 8 °C higher than air temperatures on warm sunny days (Cabot, 1999), accelerates evaporation of remaining water films on the rock surface, maintaining the required micro-environmental conditions required for continued growth of this endolithic lichen species. At this stage the lichen thallus shields the rock surface from direct contact with rainfall and its associated dissolutional processes, but subjects the same surface to a series of biological weathering mechanisms induced by lichenic metabolism.



**Figure 5.** Model for biologically-induced solution basin development on Carboniferous limestone in the Burren, Co. Clare.

### Stage 3: Biotrough formation

As the lichen matures, perithecia form within the photobiont layer and expand through the upper pseudomedulla, eventually emerging through the substratum exposing the characteristic black and white *Verrucaria baldensis* ostiole (Figure 3). Ascospore dispersal occurs via this minute apical pore and once the perithecial cavity is emptied of spores, the perithecial envelope falls out or decomposes leaving a characteristic sub-microscale biopit, approximately 0.2 mm (200 µm) in diameter (Figure 6), on the rock surface. Theoretically, other local endolithic lichens (Table II) also have the potential to produce biopits of various diameters depending on the species. Nevertheless, at the sample location, the isolated occurrences of these species make them much less geomorphologically significant than the widespread *V. baldensis*. Although *V. baldensis* has the smallest perithecia of the six species identified in the study area (c. 0.2 mm diameter), its thallus is crowded with these fruiting bodies, making it the most important of the species identified in terms of its potential geomorphological contribution. Perithecia can only form within the confines of the lichen thallus. Consequently, empty biopits cannot be reused by the lichen for further ascospore dispersal and they remain as relict bioweathering features within the substrate. However, as radial growth continues and perithecia successively form in already intensely biopitted areas, over time the concentration of biopits increases and multiple biopits may coalesce to form larger interconnected microscale depressions. Similarly, if the initial endolithic lichen dies or is succeeded, parasitized or out-competed by another endolithic lichen, biopits from both the previous and new individuals, may again amalgamate to form larger microdepressions.

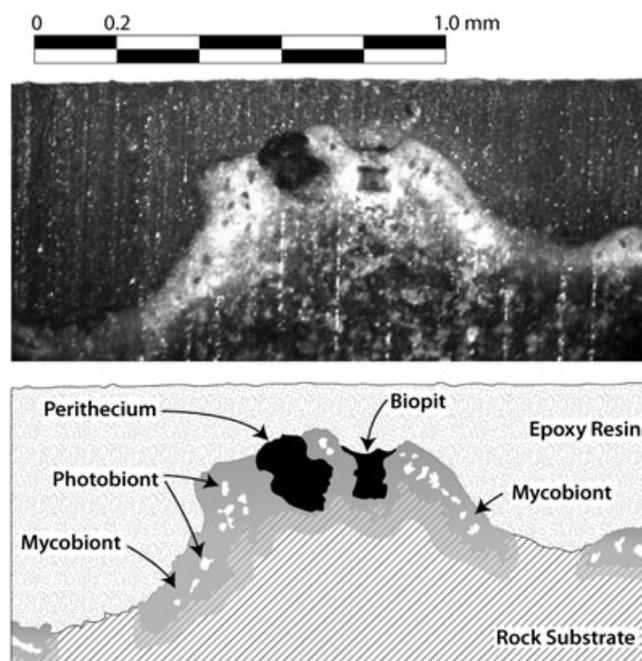
These microdepressions (Figures 4 and 7), having not been previously identified or termed in the literature, are referred to here as biotroughs, which form an irregular microtopography composed of a network of interconnected troughs, that are inferred to be the product of the amalgamation or coalescing of endolithic lichen-induced biopits (see Figure 4a). Biotroughs, forming beneath active endolithic lichen cover, have been observed on both horizontal and vertical surfaces in the Burren,

indicating that this microscale morphology is, at least initially, a form of biokarst, developing as a consequence of endolithic lichen-induced surface modification, irrespective of environmental forcing. However, on horizontal surfaces, the accumulation of water within such microdepressions may play an important role in the altering of micro-environmental conditions and the enlargement of these microscale weathering features.

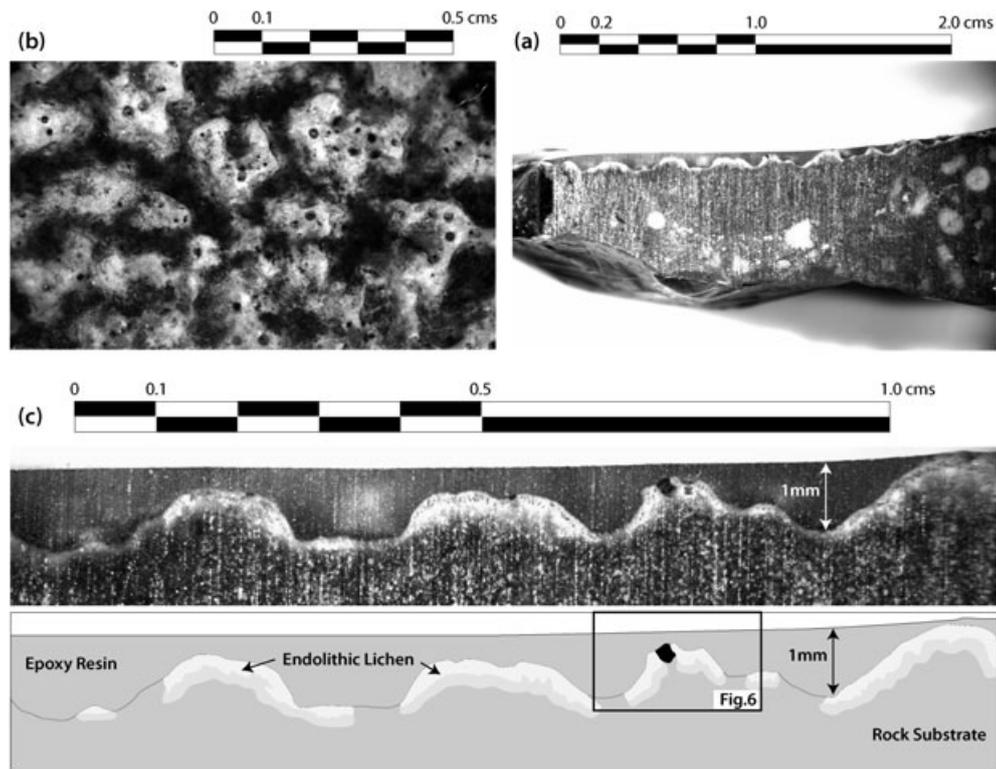
At this point in the sequence, a critical threshold or transitional point is reached when an important micro-environmental change begins to occur in the system. Water droplets or films, initially too large to penetrate the voids (c. 160–250 µm diameter) created by individual biopits, may, due to the influence of scale in fluid dynamics (Yatsu, 1988; Camuffom, 1998), now settle in the larger biotroughs altering micro-environmental conditions in the expanded cavities. At this stage, carbonic and organic acids in rainwater runoff cannot yet attack or dissolve the calcareous substrate as the intricate network of fungal hyphae in the upper pseudomedulla impedes direct contact between water and unweathered limestone. However, the presence of water in these microscale biotroughs, for increasing periods of time following rainfall events, represents a considerable challenge to the still actively metabolizing *Verrucaria baldensis* within the depressions.

### Stage 4: Biotrough enlargement

Lacking roots as an effective means of nutrient absorption, lichens depend on both atmospheric and lithic sources for essential micro- and macro-nutrients. In the absence of a waxy cuticle common in vascular plant leaves, elemental exchange can occur across the entire lichen surface, with lichens being effective scavengers of ions from dilute solutions such as runoff (Nash III, 2010). Consequently, the intermittent accumulation of water in the enlarged micro-depressions following rainfall events may inhibit gaseous exchange between the periodically submerged lichen and the atmosphere, inducing a number of physiological responses that may limit, and ultimately cause the cessation of, algal or fungal productivity. For example, water accumulation may cause the blocking of CO<sub>2</sub>



**Figure 6.** Cross-section of *Verrucaria baldensis* on Carboniferous limestone, the Burren, Co. Clare. Perithecia become deeply immersed in the lichen thallus (and consequently also in the substratum as this is an endolithic species) creating visible biopits, up to 0.25 mm in diameter when they fall out (Dobson, 2005). The perithecia in this example is 0.19 mm in diameter and extends to a depth of 0.21 mm into the limestone substrate.



**Figure 7.** *Verrucaria baldensis* on Carboniferous limestone, the Burren, Co. Clare. It is inferred that the coalescing of biopits from the existing *V. baldensis* community and previous endolithic activity, along with associated positive feedback mechanisms, has resulted in localized surface lowering giving rise to the irregular micromorphology, termed biotroughs, visible in plan view (b) and in cross-section (a) and (c). Impregnated with epoxy resin to maintain surface features intact during the cutting process, the roughest area of the sample displays up to 1 mm surface lowering relative to its surroundings. Note in (c) how endolithic lichen coverage decreases significantly and even disappears within the biotroughs.

diffusion pathways in the thallus (Palmer and Friedmann, 1990; Lange and Green, 1996; Tretiach and Geletti, 1997), or an alteration of the pH environment which intimately influences the nutrients available to the lichen. Ultimately, these processes may contribute to the gradual death of a terrestrial lichen, such as *Verrucaria baldensis*, within the troughs, leaving characteristic raised 'islands' of metabolizing lichen surrounded by micro-scale biotroughs which are up to 1 mm deep in the samples collected (Figure 7c).

Since the crystalline structure of the upper substrate is effectively bound together by fungal hyphae, the gradual decay of the endolithic lichen thalli exposes the fragmented particles, previously encased in the fungal hyphae, and underlying calcareous substrate to dissolutional processes, causing the deepening and enlarging of the biotroughs. Furthermore, when hyphae, which may have dissolved calcite to significant depths, decay, voids are left increasing the porosity of the upper substrate, effectively allowing water to infiltrate and begin dissolution, to the extent of the previous hyphal penetration. Consequently, as water percolates into the voids previously created by euendolithic lichen hyphae, surface lowering of a section of limestone previously penetrated by endolithic lichen hyphae is likely to occur much more rapidly than on a previously uncolonized surface with a different weathering inheritance.

#### Stage 5: Incipient solution basin formation

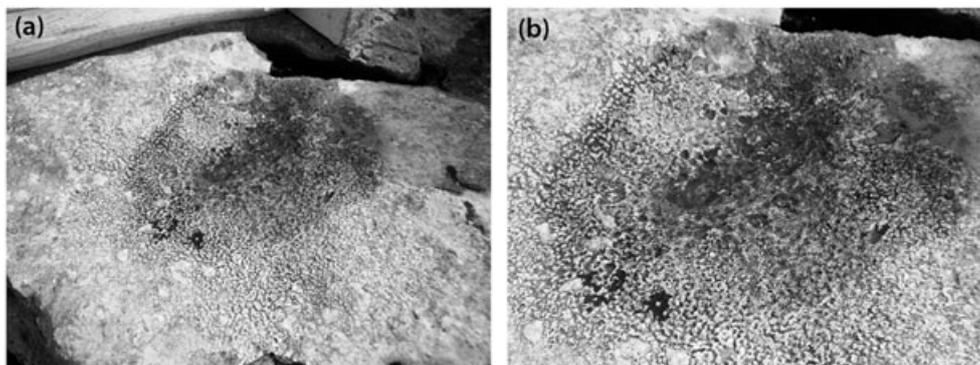
Surface lowering will be greatest towards the centre of the lichen thallus (Figure 8), i.e. at the spot of initial colonization, as this is where the lichen thallus is oldest and most intensely biopitted, and hence also where biotroughs are most likely to initially develop. Acceleration of surface lowering at the centre gives rise to incipient solution basin development. Islands of actively metabolizing *Verrucaria baldensis*, separated from

each other by a network of biotroughs, continue to biopit their increasingly smaller available substrate area and over time decrease in size, ultimately becoming submerged by standing water in the embryonic solution basin. In effect, *Verrucaria baldensis* pays a price for the extensive and successive biopitting of its substrate, which leads to its partial death with only the fringes or newest growth of the initial lichen surviving, but in time likely to be overwhelmed by solution basin expansion.

Bungartz *et al.* (2004), in a study within the arid environment of the Sonoran Desert, observed that on small specimens of caliche heavily colonized by the lichen *Verrucaria rubrocincta* with no room for lateral hyphal penetration, extensive deterioration due to successive biopitting led to microhabitat alteration and eventually resulted in thallus death. In a temperate, pluvius environment such as the Burren, in which a plethora of lithobionts coexist, this gradual change in micro-environmental conditions leads to the out-competing of one species by others more suitably adapted to those conditions.

#### Stage 6: Basin enlargement

Effectively, periodic and intermittent submersion causes the terrestrial, endolithic *Verrucaria baldensis*, more suited to dry, exposed conditions, to lose its foothold and be out-competed by organisms adapted to the changing micro-environment (e.g. free-living algae or cyanobacteria, or amphibious, gelatinous lichens such as *Collema auriforme*, *C. callopismum*, *Leptogium schraderi* and *L. plicatile*). Being regularly submerged by freshwater, many species of *Collema* and *Leptogium* can be considered amphibious lichens. Both are cyanolichens and contain the cyanobacterial genus *Nostoc*, which also occurs in a free-living state in solution basins in the Burren and has allowed these lichens to colonize microhabitats which are regularly submerged (Seaward, 2010). Colonization by such species



**Figure 8.** Sub-mesoscale surface lowering associated with perithecia-producing endolithic lichen communities leading to incipient solution basin formation. In the centre of the depression, where localized surface lowering has facilitated the accumulation of water, free-living algae, cyanobacteria and gelatinous lichen communities are likely to colonize. Note how the characteristic microtopographical pattern of biotroughs, associated with successive perithecia-producing communities, is gradually being destroyed in the centre as other processes, principally chemical dissolution by carbonic and organic acids, begin to predominate.

induces an additional series of surface biomodification processes, which contribute to the continuing development of the solution basin. The aforementioned *C. auriforme*, for example, is responsible for the mechanical detachment or plucking of fragments from the rock surface during hyphal contraction and expansion associated with wetting and drying cycles, as reported by Moses and Smith (1993).

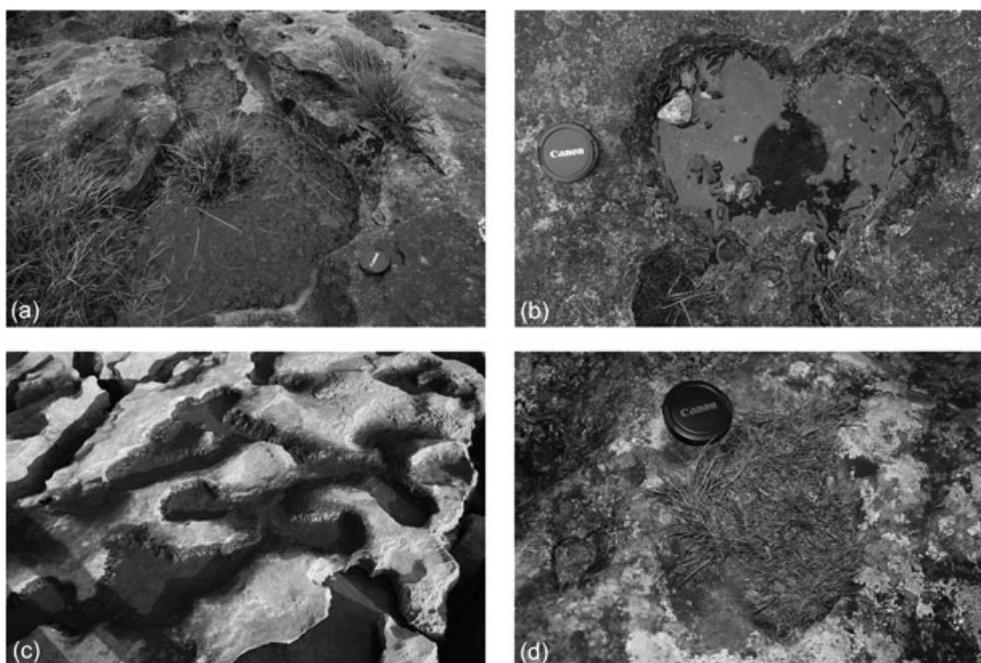
#### Stage 7: Mature solution basin

Ultimately, as the depth of the solution basin increases, water accumulates in the developing basin for increasing periods of time following rainfall events. The dissolution of calcite by dilute carbonic acid in rainwater and the biodeteriorative effects of amphibious lichens, algae and cyanobacteria cause the solution basin to mature and grow in diameter and depth (Figure 9a). As the basin develops from a sub-mesoscale feature into a mesoscale form, oval in shape with steep sides and a flat bottom, rillenstein or microrills (Ford and Williams, 2007) may develop on the vertical edges of the basin as a consequence of

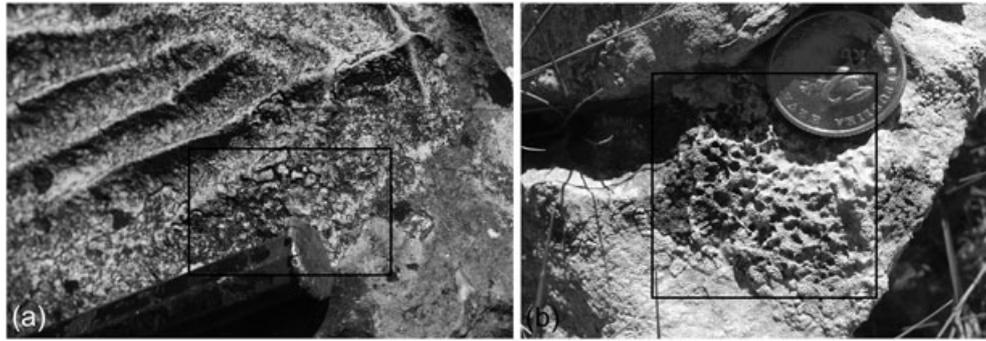
inflow. Eventually, just as biopits coalesce at the microscale, mesoscale solution basins may amalgamate to form larger basins (Figure 9b). Alternatively, outflow features such as meanderkarren may develop thereby inhibiting further lateral expansion of the basin by channelling water into adjacent grikes (Figure 9c), often creating runnels on the edges of clints in the process. Eventually, if vertical dissolution in the solution basin intersects a bedding plane, the basin may drain from below allowing the accumulation of rock fragments, aeolian dusts and organic matter, effectively giving rise to the destruction of the solution basin and colonization by grass or higher vegetation (Figure 9d).

## Discussion

This study is not suggesting that all solution basins are biologically initiated. Indeed, there is no doubt that solution basins can come about as purely solutional forms without biological mediation. Thus, solution basins may possess an element of



**Figure 9.** (a) Mature solution basin with extensive amphibious lichen colonization; (b) amalgamated solution basins; (c) meanderkarren channelling solution basin outflow; (d) relict solution basin infilled by soil.



**Figure 10.** (a) Biotrough morphologies associated with endolithic lichen biopitting at Sierra Tramuntana, Mallorca and (b) in the Dinaric karst, Dubrovnik.

equifinality, as similar forms can develop with or without biological mediation, leaving little or no evidence of the processes responsible for their initiation. Therefore, the chronological sequence proposed in this paper for biologically induced solution basin formation is only one model by which these features may arise.

By applying lichenological and geomorphological knowledge to microtopographical observations, this investigation has identified an association between sub-microscale biopitting and micro/mesoscale surface lowering. Nevertheless, with the timescales involved in biotrough and solution basin development surpassing the scope of human observation, we are only able to observe and interpret these morphologies as snapshots in time at their various stages of development. Consequently, at this stage it is not possible to demonstrate the existence of a causal link between lichen-induced biopitting and the weathering microtopography exhibited by the limestone. It must be noted that there are other processes operating within the proposed model, which although mentioned, go beyond the scope of this investigation. For example, the thalline surfaces of lichens are known to provide ideal habitats for free-living fungi, algae, bacteria and cyanobacteria. However, the possible presence (see Figure 4) and/or effects of these microorganisms within enlarging biopits and biotroughs have not been explored, with these organisms possibly aiding substrate dissolution via the excretion of organic acids. To shed light on this matter would require a detailed microbiological investigation. Similarly, a number of well-founded assumptions, though assumptions nonetheless, may need to be investigated in more detail if the proposed model is to be clarified further. For example, the precise mechanisms of fluid dynamics between biopits and water, assumed to be similar to those of pore spaces in rocks, or the precise nature and rate of endolithic hyphal decay under persistently saturated conditions.

To emphasize the relevance of geomorphological process domains, in reality we do not need to venture far from the study area for the environment to change sufficiently as to disrupt the proposed model for solution basin formation. For example, in the supratidal zones of the Burren, salts inhibit extensive endolithic lichen habitation, with coastal solution basins being morphologically distinct from their terrestrial counterparts due to marine salt crystallization cycles and halophytic microorganism activity. Nevertheless, many karst environments the world over may provide the necessary conditions for solution basins to develop both as purely solutional forms and as biologically initiated karren features. Although *Verrucaria baldensis* is climatically a wide-ranging species, not all karst areas with abundant endolithic lichen communities display microscale biotrough morphologies. The reasons for this are unknown, though petrological analysis of the sampled substrate has revealed that biotrough morphologies seem to form exclusively in sparite, i.e. fine crystalline calcite cement. Consequently,

even slight changes in substrate mineralogy, say to a predominantly micritic matrix with an abundance of allochems, may suffice to inhibit biotrough formation and explain why biotroughs may be poorly developed or absent on other calcareous surfaces with extensive *Verrucaria baldensis* coverage. Nevertheless, biotrough morphologies associated with endolithic lichen biopitting have been observed in karstic environments climatically distinct to the Burren, for example in the Balearics and in the Dinaric karst (Figure 10).

Geomorphologically, the timescales involved in solution basin formation are largely unknown but likely to range from decades to centuries depending on the environment in which they are formed. Lichenologically, the growth rate of *Verrucaria baldensis* is known only from a laboratory culture (Favero-Longo *et al.*, 2009) which, as aforementioned, is likely to be unrepresentative of the Burren environment. Added to this is the problem of endolithic growth being renowned for its slowness if direct lichenometric techniques were to be employed to estimate a growth rate for this species. Furthermore, with endolithic growth rates varying significantly under even slightly different environmental conditions, an environment-specific investigation would be the only way to shed light on the matter. Finally, as with growth rates, the rate of perithecia production and the timescales involved in biotrough formation are largely unknown. Ultimately, many of these questions would be best tackled with better lichenological knowledge and within an ecological framework. Consequently, interdisciplinary studies, incorporating geomorphologists, lichenologists, ecologists and microbiologists, are without doubt the best way forward in expanding our understanding of the precise role of lithobionts in the formation of mesoscale karst landforms.

## Conclusion

This study proposes a model to explain the initiation of mesoscale solution basin formation through the action of organisms operating at the microscale through the development of biopits and eventually biotroughs, the latter being a previously unidentified micromorphology of biokarstic origin and a key stage in the lichenic initiation of solution basin development. Observed on both horizontal and vertical surfaces, biotroughs on vertical or significantly inclined surfaces are unexploited by water and poorly developed. Consequently, lichenic coverage is likely to bioprotect the underlying substrate during the lifespan of the organism due to the hyphal binding of the crystalline rock structure. By contrast, biotroughs on level surfaces may be exploited by water films, whose presence over prolonged periods may alter micro-environmental conditions and cause the decay of endolithic lichen thalli, eventually inducing rapid localized surface lowering and the initiation of solution basin development.

It is important to remember that when observing the lichen–rock interface at any one moment in time, we are effectively looking at a snapshot of what is a dynamic and constantly changing micro-environment operating on a timescale sufficiently long to make human observation problematic. Visible biopitting on a rock surface may not necessarily have been caused by the lichen community presently living on that surface. As with macrotopographies and landscapes, microtopographies are a product of the historical weathering inheritance of that particular rock surface.

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## References

- Ariño X, Ortega-Calvo JJ, Gomez-Bolea A, Saiz-Jimenez C. 1995. Lichen colonisation of the Roman pavement at Baelo Claudia (Cadiz, Spain): biodeterioration vs. bioprotection. *The Science of the Total Environment* **167**: 353–363.
- Bungartz F, Garvie LAJ, Nash III TH. 2004. Anatomy of the endolithic Sonoran Desert lichen *Verrucaria rubrocincta* Breuss: implications for biodeterioration and biomineralisation. *The Lichenologist* **36**(1): 55–73.
- Cabot D. 1999. *Ireland*. The Bath Press: Bath.
- Camuffo D. 1998. *Microclimate for Cultural Heritage, Developments in Atmospheric Science*, 23. Elsevier: Amsterdam.
- Carter NEA, Viles HA. 2003. Experimental investigations into the interactions between moisture, rock surface temperatures and an epilithic lichen cover in the bioprotection of limestone. *Building and Environment* **38**: 1225–1234.
- Carter NEA, Viles HA. 2004. Lichen hotspots: raised rock temperatures beneath *Verrucaria nigrescens* on limestone. *Geomorphology* **62**: 1–16.
- Carter NEA, Viles HA. 2005. Bioprotection explored: the story of a little known earth surface process. *Geomorphology* **67**: 273–281.
- Chen J, Blume HP, Beyer L. 2000. Weathering of rocks induced by lichen colonisation – a review. *Catena* **39**: 121–146.
- Cooks J, Otto E. 1990. The weathering effects of the lichen *Lecidea* Aff. *Sarcogyniodes* (Koerb.) on Magaliesberg quartzite. *Earth Surface Processes and Landforms* **15**: 491–500.
- Danin A. 1993. Pitting of calcareous rocks by organisms under terrestrial conditions. *Israel Journal of Earth Sciences* **41**: 201–207.
- Danin A, Gerson R, Garty J. 1983. Weathering patterns on hard limestone and dolomite by endolithic lichens and cyanobacteria: supporting evidence for aeolian contribution to terra rossa soil. *Soil Science* **136**(4): 213–217.
- Dobson FS. 2005. *Lichens, an Illustrated Guide to the British and Irish Species*, 5th edn. The Richmond Publishing Co. Ltd: Slough.
- Favero-Longo SE, Borghi A, Tretiach M, Piervittori R. 2009. In vitro receptivity of carbonate rocks to endolithic lichen-forming aposymbionts. *Mycological Research* **113**: 1216–1227.
- Fiol L, Fornós JJ, Ginés A. 1996. Effects of biokarstic processes on the development of solutional rillenkarren in limestone rocks. *Earth Surface Processes and Landforms* **21**: 447–452.
- Ford DC, Williams PW. 2007. *Karst Hydrogeology and Geomorphology*. Wiley: Chichester.
- Fry EJ. 1922. Some types of endolithic limestone lichens. *Annals of Botany* **144**(36): 541–562.
- Gehrmann C, Krumbein WE, Petersen K. 1992. Endolithic lichens and the corrosion of carbonate rocks. *International Journal of Mycology and Lichenology* **5**: 37–48.
- Geikie A. 1893. *Textbook of Geology*. Macmillan: London.
- Gueidan C, Savić S, Thüs H, Roux C, Keller C, Tibell L, Prieto M, Heiðmarsson S, Breuss O, Orange A, Fröberg L, Amtøft Wynns A, Navarro-Rosinés P, Krzewicka B, Pykälä J, Grube M, Lutzoni F. 2009. Generic classification of the Verrucariaceae (Ascomycota) based on molecular and morphological evidence: recent progress and remaining challenges. *Taxon* **58**(1): 184–208.
- Hale ME. 1973. Growth. In *The Lichens*, Ahmadjian V, Hale ME (eds). Academic Press: London; 473–492.
- Hall K, Guglielmin M, Strini A. 2008. Weathering of granite in Antarctica: I. Light penetration into rock and implications for rock weathering and endolithic communities. *Earth Surface Processes and Landforms* **33**: 295–307.
- Hawksworth DL. 1988. Coevolution of fungi with algae and cyanobacteria in lichen symbiosis. In *Coevolution of Fungi with Plants and Animals*, Pirozynski KA, Hawksworth DL (eds). Academic Press: London; 125–148.
- Khodosovtsev AY. 1995. Lichens on monuments in the southern part of Ukraine. *Proceedings, 3rd International Conference on Biodeterioration of Cultural Property*, 4–7 July, Bangkok, Thailand; 335–240.
- Lange OL, Green ATG. 1996. High thallus water content severely limits photosynthetic carbon gain of central European epilithic lichens under natural conditions. *Oecologia* **108**: 13–20.
- McCarthy PM. 1983. The composition of some calcicolous lichen communities in the Burren, Western Ireland. *The Lichenologist* **15**(3): 231–248.
- Met Éireann. 2010. Climate Averages and Extremes, Dublin: Met Éireann. <http://www.met.ie/climate/shannonairport.asp> [3 December 2010].
- Mitchell GF. 1981. The Quaternary – until 10,000 BP. In *A Geology of Ireland*, Holland CH (ed.). Scottish Academic Press: Edinburgh; 235–258.
- Mohammadi P. 2008. Biodeterioration of ancient stone materials from the Persepolis monuments (Iran). *Aerobiologia* **24**(1): 27–33.
- Moles NR, Moles RT. 2002. Influence of geology, glacial processes and land use on soil composition and Quaternary landscape evolution in the Burren National Park, Ireland. *Catena* **47**: 291–321.
- Moses CA, Smith BJ. 1993. A note on the role of the lichen *Collema auriforma* in solution basin development on a carboniferous limestone substrate. *Earth Surface Processes and Landforms* **18**: 363–368.
- Mottershead D, Lucas G. 2000. The role of lichens in inhibiting erosion of a soluble rock. *The Lichenologist* **32**(6): 601–609.
- Nash III TH. 2010. Nutrients, elemental accumulation, and mineral cycling. In *Lichen Biology*, 2nd edn, Nash TH. (ed.). Cambridge University Press: Cambridge; 236–253.
- Palmer Jr RJ, Friedmann EI. 1990. Water relations, thallus structure and photosynthesis in Negev Desert lichens. *New Phytologist* **116**: 597–603.
- Pinna D, Salvadori O, Tretiach M. 1998. An anatomical investigation of calcicolous endolithic lichens from the Trieste karst (NE Italy). *Plant Biosystems* **132**: 183–195.
- Portero de la Torre R, Bolívar Galiano F, Casares Porcel M, Cultrone G. 2004. Estudio multidisciplinar del biodeterioro por líquenes en las fachadas del Colegio Máximo de la Cartuja de Granada. In *Actas XV Congreso de Conservación y Restauración de Bienes Culturales*. Liria: Murcia; 845–852.
- Seaward MRD. 2010. Environmental role of lichens. In *Lichen Biology*, 2nd edn, Nash TH (ed.). Cambridge University Press: Cambridge; 276–300.
- Sleeman AG, Scanlon RP, Pracht M, Caloca S. 2008. Landscape and Rocks of The Burren: Bedrock Geological Map 1:50,000 scale. Geological Survey of Ireland: Dublin.
- Tretiach M. 1995. Ecophysiology of calcicolous endolithic lichens: progress and problems. *Giornale Botanico Italiano* **129**: 159–184.
- Tretiach M, Geletti A. 1997. CO<sub>2</sub> exchange of the endolithic lichen *Verrucaria baldensis* from karst habitats in northern Italy. *Oecologia* **111**: 515–522.
- Viles HA. 1995. Ecological perspectives on rock surface weathering: towards a conceptual model. *Geomorphology* **13**: 21–35.
- Viles HA. 2001. Scale issues in weathering studies. *Geomorphology* **41**: 63–72.
- Yatsu E. 1988. *The Nature of Weathering*. Sozoshia: Tokyo.