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Lichens of the Namib Desert, South West Africa/Namibia

I. The chasmoendolithic habitat

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DUPLICATE

ABSTRACT

The habitat, initial stages of colonization and morphological features of a chasmoendolithic species of *Lecidea* inhabiting cracks in quartz are discussed and illustrated with SEM micrographs and photomicrographs. Colonized quartz pebbles and stones form part of the desert pavement and quartz outcrops in the Namib Desert. Mechanical and chemical weathering of the quartz by the endolithic lichen is shown. Different possible advantages of the chasmoendolithic habitat occupied by the chasmoendolithic *Lecidea* species are pointed out.

KEY WORDS

Lichens, Weathering, Endolithic, Chasmoendolithic, Quartz, Namib Desert.

INTRODUCTION

Lichens are poikilohydric organisms, tolerant to desiccation (Lange, 1953) and extremes in temperature (Kappen, 1973). Publications by Hale (1983), Hawksworth & Hill (1984), Kershaw (1985) and those edited by Ahmadjian & Hale (1973), Seaward (1977) and Brown (1985) cover several aspects of the physiology, biology and ecology of mainly epilithic lichens.

Friedmann *et al.* (1967) and Friedmann (1982) respectively discussed the occurrence of endolithic algae in the Negev Desert and cryptoendolithic organisms in Antarctica. The cryptoendolithic microbial environment was discussed by Friedmann *et al.* (1987), the lithobiontic microbial habitat by Friedmann & Ocampo-Friedmann (1984), the taxonomy of fertile stages of cryptoendolithic lichens by Hale (1987) and abiotic weathering by cryptoendolithic microorganisms by Friedmann & Weed (1987). Recent findings on cryptoendolithic lichens were reviewed by Lawrey (1984).

Apart from physiological aspects, the successful growth of lichens under extreme environmental conditions such as hot or cold deserts is partly due to ecological reasons (Kappen & Friedmann, 1983a). In extreme rainless deserts such as the Namib Desert (Walter, 1986), lichens often exist in the shade of rocks, occur in abundance against mountain slopes, on outcropping rocks, or desert pavement. Lichen habitats in the

so called mist oases of the Namib Desert are commonly exposure dependent. A considerable number of epilithic saxicolous lichen species cover different substrates in the mist oases. Moisture levels in such oases are generally higher, while temperatures may be more moderate than the surrounding area (Kappen, 1985).

Besides epilithic lichens, bare rocks and desert pavement of the central and northern Namib Desert provide ample substrates for colonization by several lithobiontic lichen species. These lichens colonize the interior of porous rocks and cracks in non porous rocks. Lithobiontic lichens represent a highly specialized adaptation to the desert environment. Contrary to observations made in the Namib Desert, mainly endolithic lichen species are present in the dry valleys of southern Victoria Land, Antarctica (Friedmann *et al.*, 1980). The number of epilithic lichen species in the Namib Desert far outnumbers the endolithic species. According to Friedmann *et al.* (1980) environmental conditions in the dry valleys of Victoria Land are too harsh to support epilithic growth. The occurrence of endolithic lichens in the Namib, amongst a profusion of epilithic lichens, suggests the presence of conditions favourable to colonization and growth by both groups of lichen species and the efficiency in which lichens exploit potential habitats in the Namib Desert.

In this preliminary report only a few general aspects will be dealt with about the varied endolithic lichen growth forms present in the central Namib Desert. The discussion will deal specifically with an undescribed chasmoendolithic species of *Lecidea* growing in quartz. A detailed description of the chasmoendolithic *Lecidea* species will be published in a taxonomical journal.

Material and methods

Material

Examples of the chasmoendolithic *Lecidea* species growing in quartz were collected by the author's wife on the gravel plain east of Henties Bay, South West Africa/Namibia. Quartz pebbles in which the chasmoendolithic lichen grows, form part of the quartz outcrops and desert pavement of the central and northern Namib Desert. Representative specimens are deposited in the herbarium of the University of the North.

Methods

Microphotographs

Microphotographs were taken with a Wild M5 A stereomicroscope fitted with a Wild MPS 55 photomicrographic system.

Scanning Electron Microscopy

Artificially removed quartz fragments, colonized by the endolithic lichen, were attached to aluminium stubs by double sided tape. The specimens were kept in a desiccator for 48 hours, before coating with gold in a Bio-Rad Polaron E 5150 coating system. A Hitachi S-450 scanning electron microscope (SEM) was used to study the specimens.

Results and discussion

Lichen representatives of all the groups of endolithic growth forms proposed by Golubic *et al.* (1981), occur regularly in the Namib Desert. The endolithic lichen species mainly belong to the genera *Buellia* and *Lecidea*. Representatives of the endolithic growth forms collected in the Namib Desert include chasmoendolithic species which colonize fissures and cracks in rocks (Fig. 1), cryptoendoliths which colonize structural cavities within rocks and an euendolithic *Buellia* species which actively penetrates into calcite, forming hollows which conform to thalli of the species.

Colonization of quartz

Propagules of the chasmoendolithic *Lecidea* species colonize fine cracks (Fig. 2) or small depressions on the surface of quartz. The ultimate fate of lichen propagules

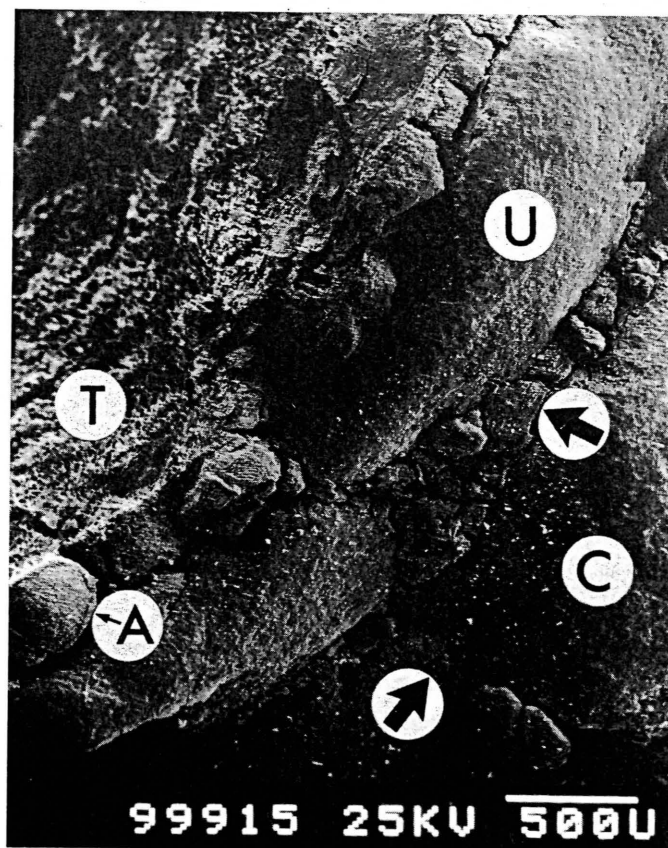


Figure 1: Quartz surface colonized by a chasmoendolithic *Lecidea* species. Arrows = colonized cracks. A = apothecium. U = uncolonized quartz surface. C = quartz fragment colonized on all sides by the chasmoendolithic *Lecidea* species. T = thallus of the colonizing chasmoendolithic lichen visible after removal of the covering quartz fragment.

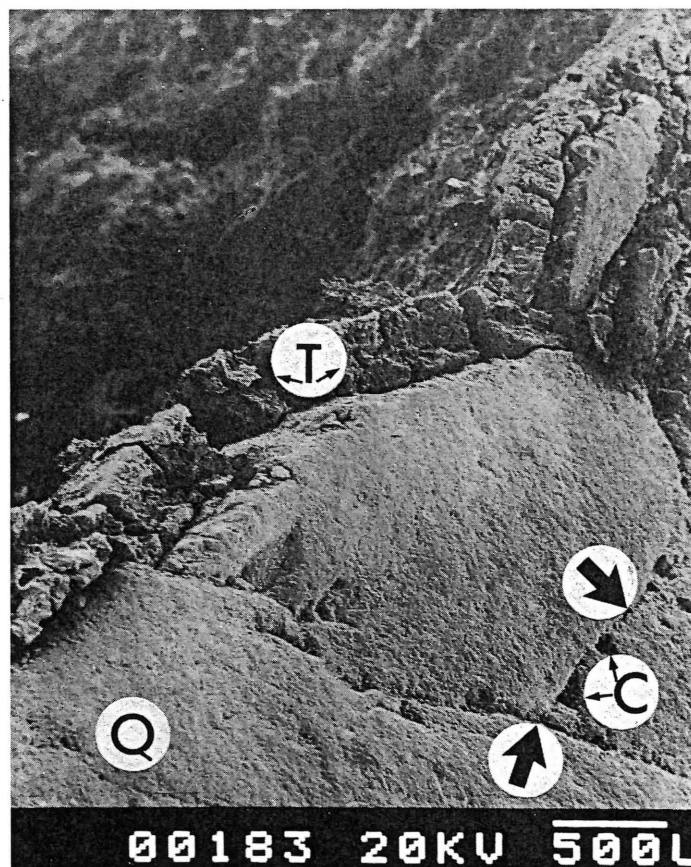


Figure 2: Colonizing propagules of the chasmoendolithic *Lecidea* species. T = part of the thallus of the chasmoendolithic *Lecidea* species. Large arrows show crack being colonized. C = cavities formed through weathering of the substrate by the colonizing lichen. Q = unaffected surface of the quartz.

in depressions on the surface of quartz is still unknown. Established propagules in minute cracks are able to actively weather and penetrate cracks in quartz (Fig. 2). Deducting from the results shown in Figs. 3 to 5, it is suggested that weathering and widening of cracks in the quartz take place by both chemical (Fig. 3) and mechanical processes (Figs. 4, 5A & 5B). This deduction is based on the presence of quartz fragments along colonized cracks (Fig. 4) and in the medullary layer of the chasmoendolithic lichen (Figs. 5A & 5B). Quartz fragments in the medullary layer are chemically weathered by the lichen. The effects of chemical weathering on quartz by the chasmoendolithic lichen are visible alongside the edge of the quartz fragment shown in Figs. 3 & 5B. Natural weathering processes may also contribute to widening of the crack.

Morphology of the lichen

Inspection of localized dark gray to blackish discolorations in quartz on the gravel plains of the Namib Desert, often reveals the existence of the chasmoendolithic *Lecidea* species in the quartz. Closer examination of such cracks in the quartz may show the external part of the lichen thallus on which apothecia may be present (Figs. 6 & 1).

Microscopical examination of quartz colonized by the chasmoendolithic lichen species revealed that the externally visible part of the lichen thallus consists of varying numbers of pulvinate areoles (Fig. 1). The alignment of the areoles (containing green algae and cyanobacteria) follows the contours of the crack (Fig. 1). Figure 1 also shows that the diameter of individual areoles varies considerably. The studied material did not include any examples where the chasmoendolithic *Lecidea* species grew out of cracks to colonize the surrounding quartz surface. Individual areoles are

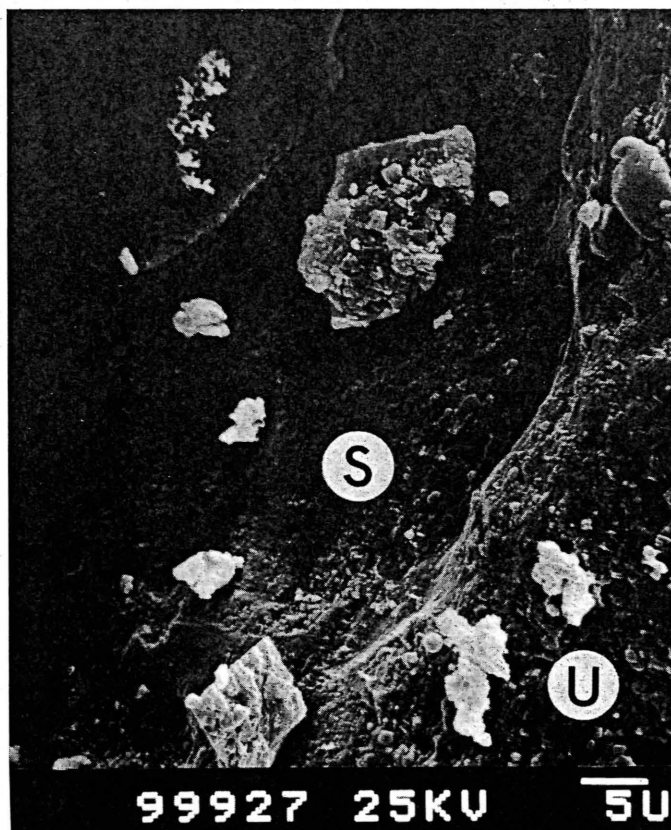


Figure 3: Smooth edge (S) of colonized crack in quartz as a result of chemical weathering by the chasmoendolithic *Lecidea* species. U = uncolonized surface of the quartz.

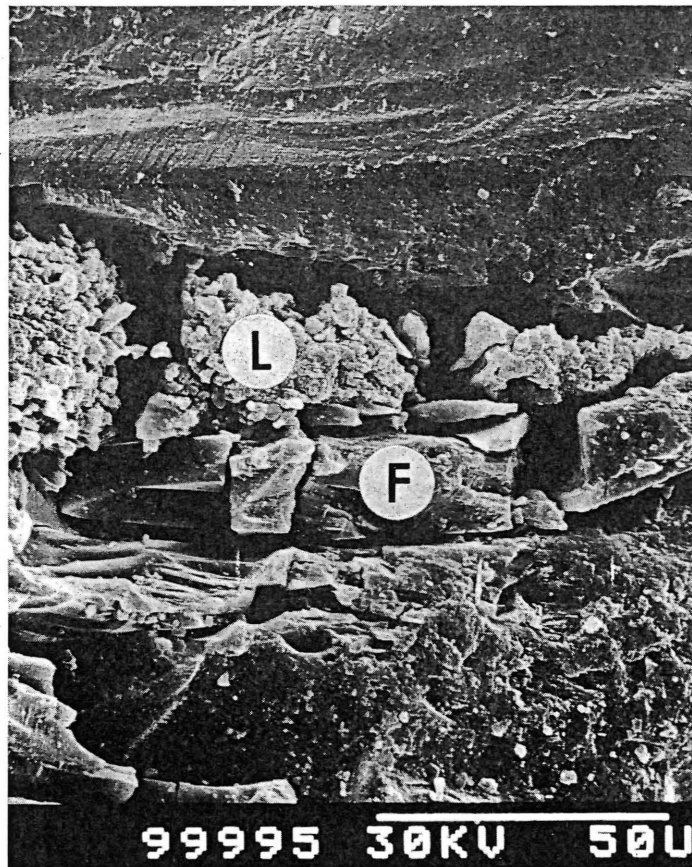


Figure 4: Fragments of quartz (F) in a crack due to mechanical forces exerted by the colonizing lichen.
L = areole of colonizing chasmoendolithic lichen.

sub-rectangular (Fig. 7), vary in size, and may be up to 1,6 mm in diameter and up to 2,0 mm high. Basally the areoles extend into the crack as an undifferentiated mass of interwoven, crowded white hyphae (Fig. 8). Areoles are adaptations to alternate wetting and drying regimes (Hawksworth & Hill, 1984).

Areoles of the chasmoendolithic *Lecidea* species are not clearly differentiated into layers. A cortex is formed at the surface of individual areoles by slightly gelatinized hyphae. No epicortex is present and the ends of vertical hyphae, packed and slightly cemented together, form the loosely organized cortex. The cortex, light brown in colour, has a knobby surface and quartz fragments are often present in this layer (Fig. 4). Areoles of the chasmoendolithic *Lecidea* species form only a small portion of the whole thallus and are the only portion of the thallus directly exposed to the environment.

Cells of the green photobiont are mainly present in the upper part of areoles, embedded in a layer of slightly gelatinized hyphae. The amount of sunlight reaching the photobiont layer depends in part on characteristics of the rock in which the lichen grows and in part on characteristics of the cortex. This in turn influences morphological characteristics, such as the distribution of the photobiont cells within the thallus. Unicellular species of cyanobacteria are often interspersed in the medulla. Gelatinous clumps containing yellowish cell associations and filamentous types of cyanobacteria are regularly present in the interior of the crack where, depending on the depth of the crack, mycobiont hyphae may be present.

The medulla consists of more loosely interwoven hyphae than those of the cortex. It extends into the crack as a mass of white hyphal threads loosely arranged into a

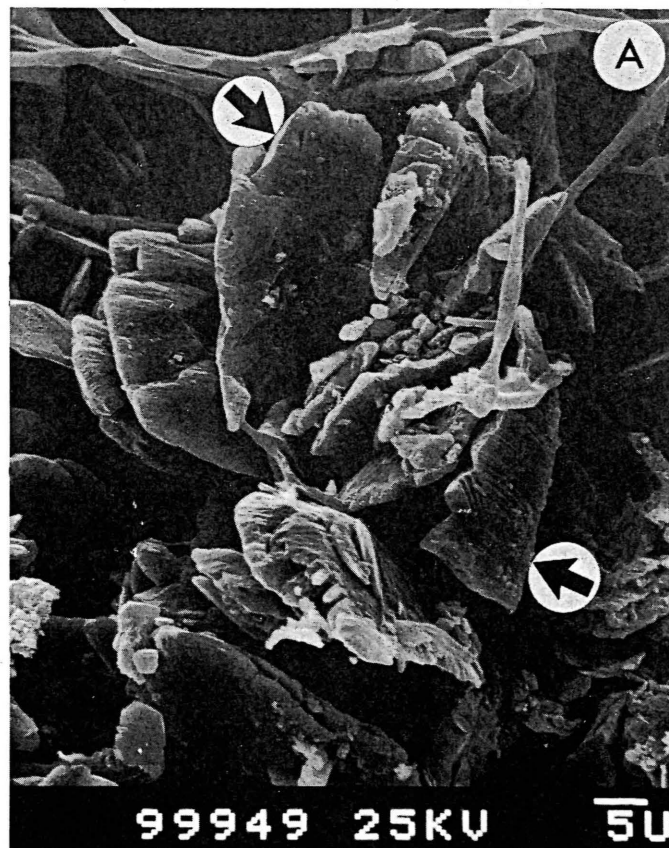


Figure 5A: Presence and colonization of quartz fragments in the medullary layer of the chasmoendolithic *Lecidea* species. A: Loose quartz fragments (arrows) in the medullary layer of the chasmoendolithic *Lecidea* species. B: Attachment of mycobiont hypha (arrow) from the medullary layer onto a quartz fragment. C = cluster of calcium oxalate enveloped by medullary hyphae.



Figure 5B.

cottony layer. The inner part of the medulla is more loosely interwoven than immediately below the cortex. This colonizing layer of the lichen may extend up to 10 mm into the crack and forms the bulk of the lichen thallus. Medullary hyphae within the crack are weakly gelatinized. The medulla links individual areoles. In cross section the shape of the thallus of the chasmoendolithic *Lecidea* species resembles a wedge in that it tapers from the upper surface of the areoles, which consist of numerous hyphae, to a single layer of innermost medullary hyphae within the crack. In the upper part of the areoles, gelatinized medullary hyphae often merge to form platelike structures (Fig. 9) on the sides of cracks.

The presence of a large number of crystals, differing in origin, shape and chemical composition (Figs. 10A & 10B) is characteristic of the medullary layer. Some of these crystals are probably formed as a result of chemical weathering of the substrate. Different forms of calcium oxalate hydrates, such as weddellite and whewellite (Figs. 10A & 10B), are formed in the medulla of the chasmoendolithic lichen. Clusters of calcium oxalate crystals enveloped by hyphae (Fig. 11) are a regular feature of the

medullary layer. Such clusters are usually ovoid in shape and may be up to 75 μm in length and 50 μm wide. Both calcium oxalate and weakly soluble lichen substances, which are abundantly present in the medulla, contribute to the chemical weathering of rocks by lichens (Syers & Iskandar, 1973). According to Hale (1983) it is the ever present calcium oxalate, a common storage product, which contributes the most to chemical weathering of substrates by lichens.

Wadsten & Moberg (1985) ascribed the formation of calcium oxalate to the need of the lichen to dispose of an excess of calcium. They also observed that the presence of calcium oxalate on lichens is more abundant in lichens from dry sites than elsewhere. The two authors hypothesized that the zeolitic water contained in weddellite may become available to lichens containing weddellite. An addition to the implicit role calcium oxalate plays in the chemical weathering of quartz by the chasmoendolithic *Lecidea* species, the lichen may according to the hypothesis of Wadsten & Moberg (1985) benefit from the zeolitic water contained in weddellite. Could the clusters of calcium oxalate crystals present in the medulla of the chasmoendolithic lichen (Figs. 5B & 11) function as both water reservoirs and play a role in the chemical weathering of quartz too?

Hyphae of the medulla attach the chasmoendolithic *Lecidea* species to the substrate and keep surrounding fragments of the quartz together underneath which the chas-

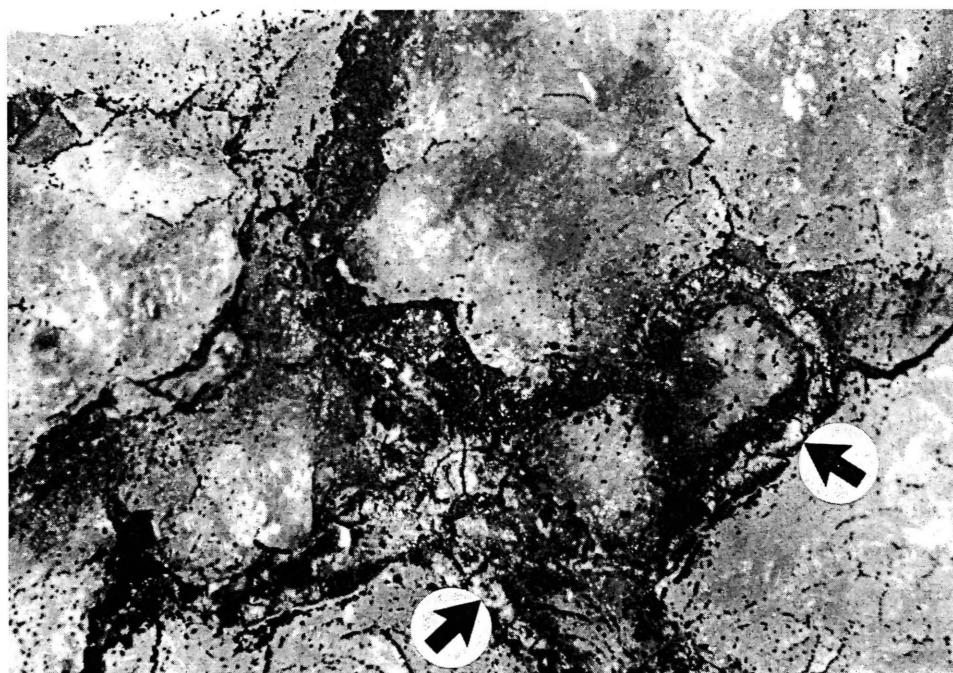


Figure 6: Externally visible part of the thallus of a chasmoendolithic *Lecidea* species (arrows). Original magnification = 6X.



Figure 7: Lateral surface view of areoles (arrows) of the thallus of a chasmoendolithic *Lecidea* species. Portion shown in the figure usually covered by the substrate in which the species grows.

moendolithic lichen grows. Mechanical pressure exerted by the colonizing chasmoendolithic lichen in combination with biological and natural weathering processes form the fragments surrounding the lichen. The physical pressure exerted by the wedge-shaped thallus of the colonizing chasmoendolithic lichen is due to an increase in volume of swollen mycobiont hyphae during wet periods.

Physiological and ecological advantages of the chasmoendolithic habitat.

Microorganisms living inside rocks in hot or cold deserts exist in severe environments characterized by extreme environmental conditions. Desert organisms are also exposed to high intensities of solar radiation (Louw & Seely, 1982).

Cryptoendolithic lichens do not have special physiological adaptations to extremes in temperatures (Kappen & Friedmann, 1983b). They too, have to respond to environ-

mental changes by speedily turning their metabolic activities on and off (Friedmann, 1982). A survival strategy employed by some microorganisms is to withdraw into the cryptoendolithic niche, where a comparatively mild environment (McKay & Friedmann, 1985), the nannoclimate according to Friedmann & Ocampo-Friedmann (1984), prevails. Louw & Seely (1982) used the term "escape" to describe such action by desert organisms. The comparative mildness of the nannoclimate is probably the most important feature responsible for the utilization of cryptoendolithic niches by microorganisms (Friedmann, 1982). In order to achieve this, lichens in contrast to unicellular algae and cyanobacteria, have to change morphologically from a plectenchymateous to a filamentous growth form. These changes in mode of growth enable lichens to colonize microscopic spaces inside porous rocks or in cracks in non-porous rocks (Kappen & Friedmann, 1983b).

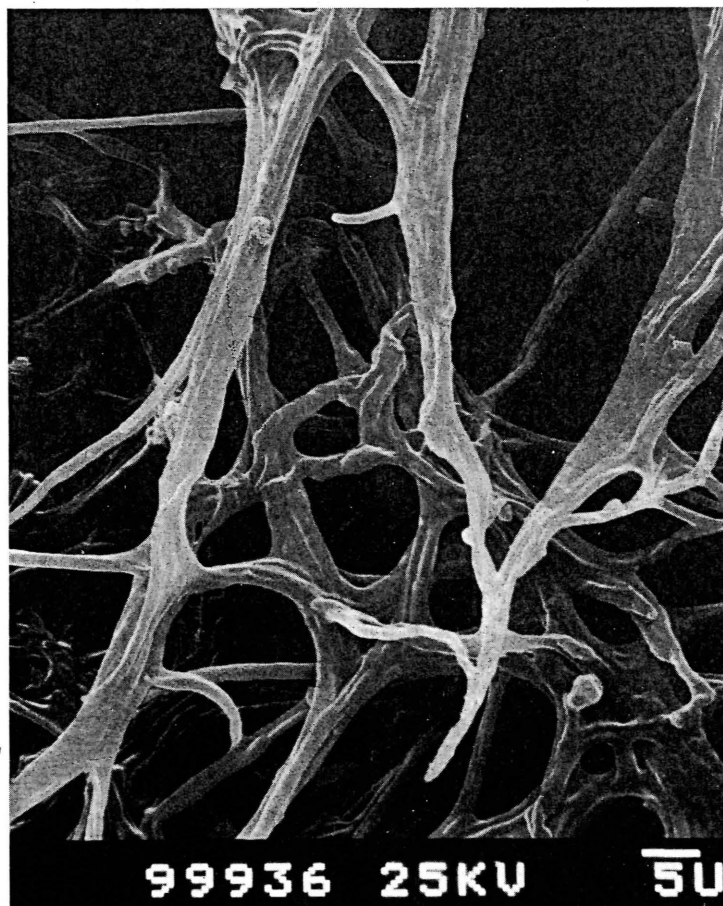


Figure 8: Arrangement and degree of gelatinization of medullary hyphae of the chasmoendolithic *Leci-
dea* species within a colonized crack.

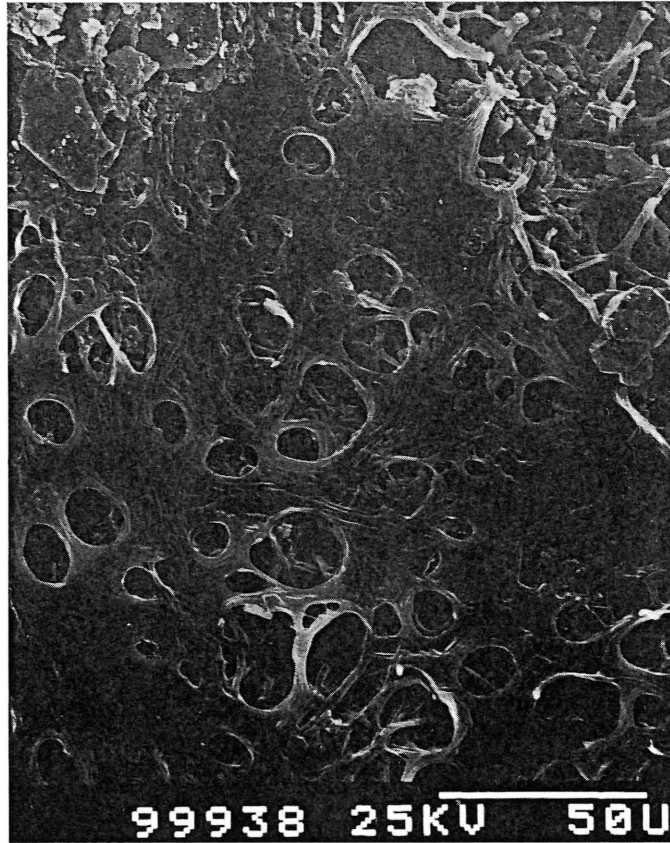


Figure 9: Platelike structures near the upper part of areoles. The structures are formed by hyphae that fuse together.

Condensing dew is a major source of water for endolithic (Friedmann, 1971) and epilithic (Rogers, 1977) microorganisms in most of the hot deserts of the world. Melting snow is of crucial importance to endoliths in the dry valleys of the Antarctic (Friedmann, 1978). In the Namib Desert, however, fog precipitation and condensing dew are major sources of moisture for both endolithic and epilithic lichens. The former source of water is probably more important than the latter, because of the frequent occurrence and persistence of fog during the early part of the morning. In certain parts of the Namib Desert the annual amount of fog precipitation exceeds the annual amount of rainfall which is between nine and 27 mm (Walter, 1986). Swakopmund for example receives 40 - 50 mm of fog precipitation per year. Fog occurs about 200 days per year at Swakopmund, which results in an average daily amount of fog precipitation of 0,2 - 0,7 mm (Walter, 1986). Fog precipitation is, therefore, more evenly distributed throughout the year than rainfall incidents

(Walter, 1936). Contrary to the capability of most higher plants in the Namib Desert, lichens are well adapted to exploiting such small amounts of precipitation. It is therefore not surprising that the distribution of lichens in the Namib Desert closely follows the distribution of fog.

The cortex of lichens serves both as a protective and absorptive layer which absorbs moisture and dissolved substances which may land on it. Lichens as a group do not have any special water retention capabilities but through modifications in their morphological structure may achieve better water relations in nature (Hale, 1983; Rundel, 1987). According to Rundel (1987) loose medullary structures and thin cortical layers associated with members of the Rocellaceae in coastal fog zones, suggest morpho-

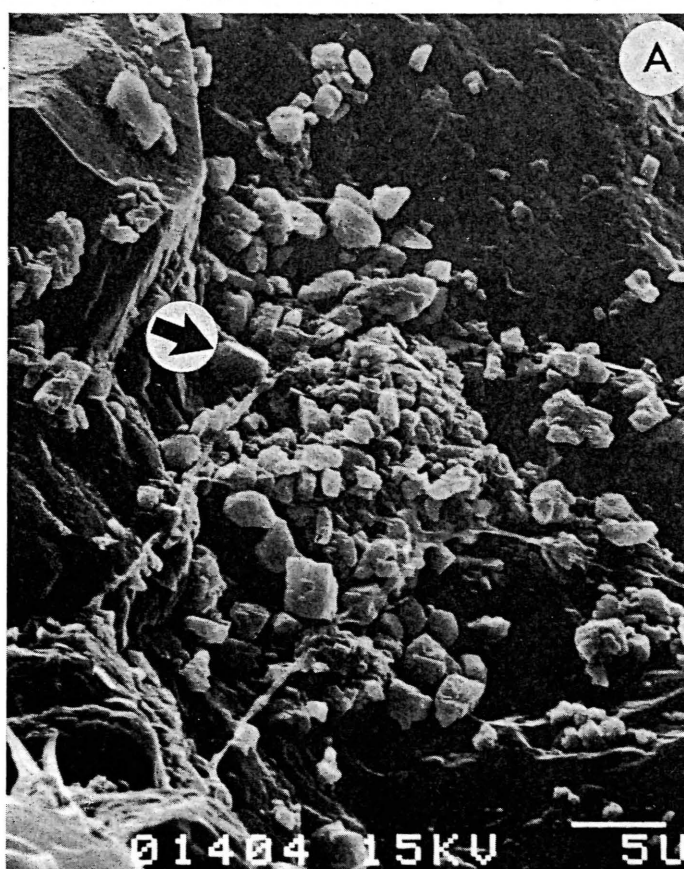


Figure 10A: Different types of calcium oxalate crystals observed in the medullary layer of the chasmodolithic *Lecidea* species. A: Assortment of crystals on the interior surface of the colonized quartz. Arrow = crystal resembling weddellite crystal type 1. B: Different types of crystals amidst medullary hyphae. Arrow = crystals resembling whewellite. Identification of crystals based on the work of Wadsten & Moberg (1985).



Figure 10 B.

logical modifications to maximize rates of water uptake. The morphology of the chasmoendolithic *Lecidea* species suggests a similar adaptation. Any reduction in thallus resistance which results in an increase in rates of water uptake will likewise increase rates of water loss (Rundel, 1987). However the chasmoendolithic lichen species under discussion may have a special advantage, contrary to epilithic lichens, in that impermeable quartz covers varying portions of the thallus. The limitation of water loss from the thallus to only a small portion of the thallus directly exposed to the surrounding atmosphere, probably prolongs the physiologically active (wet) state of such a lichen thallus. The decrease in thallus area directly exposed to the surrounding atmosphere, may compensate for an increase in rates of water loss brought about by morphological adaptations of the chasmoendolithic *Lecidea* species.

Besides water droplets which precipitate directly on the cortex of the chasmoendolithic *Lecidea* species, the lichen will additionally benefit from run-off water from the surface of the surrounding quartz which may accumulate in colonized cracks of

the quartz. The chasmoendolithic *Lecidea* species thus maximizes the rate of moisture capture by using the high surface to volume ratio afforded by the chasmoendolithic habitat.

Considering the above mentioned advantages of the chasmoendolithic habitat and habit, the chasmoendolithic *Lecidea* species may even be more suitably adapted than most other epilithic lichen growth forms in the Namib Desert in exploiting small amounts of moisture.

According to Friedmann (1980) temperatures of rock surfaces exposed to solar radiation during the day can rise significantly above air temperature. He also found that rock temperatures at night are similar to the ambient temperature, a feature that might be of importance to saxicolous and endolithic lichens of the Namib Desert in

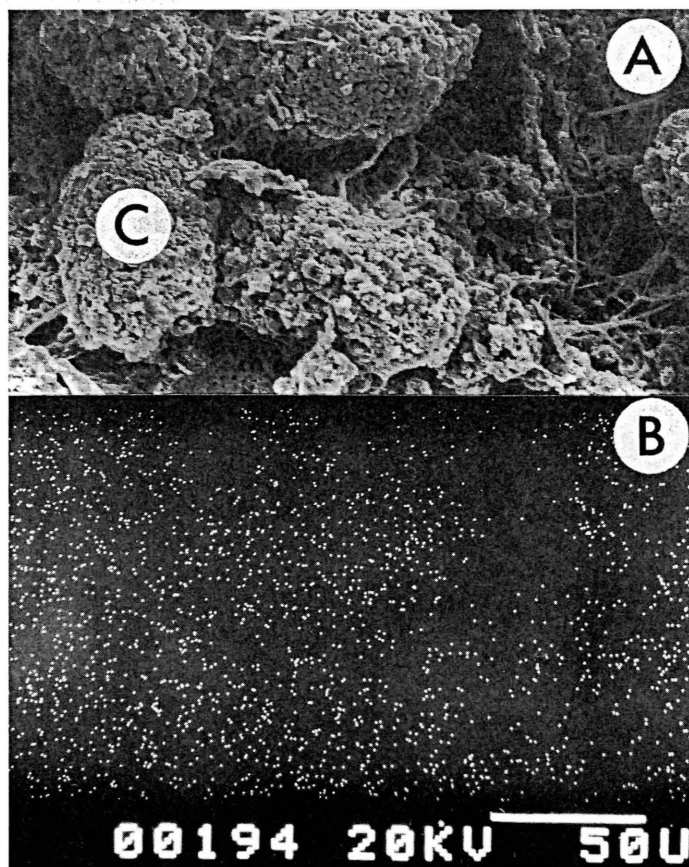


Figure 11: A: Presence of clusters (C) of calcium oxalate enveloped by medullary hyphae (A). B: Mapping of area shown in Fig. 11A for the presence of calcium. Shape of calcium containing clusters shown in Fig. 11A are visible in Fig. 11B.

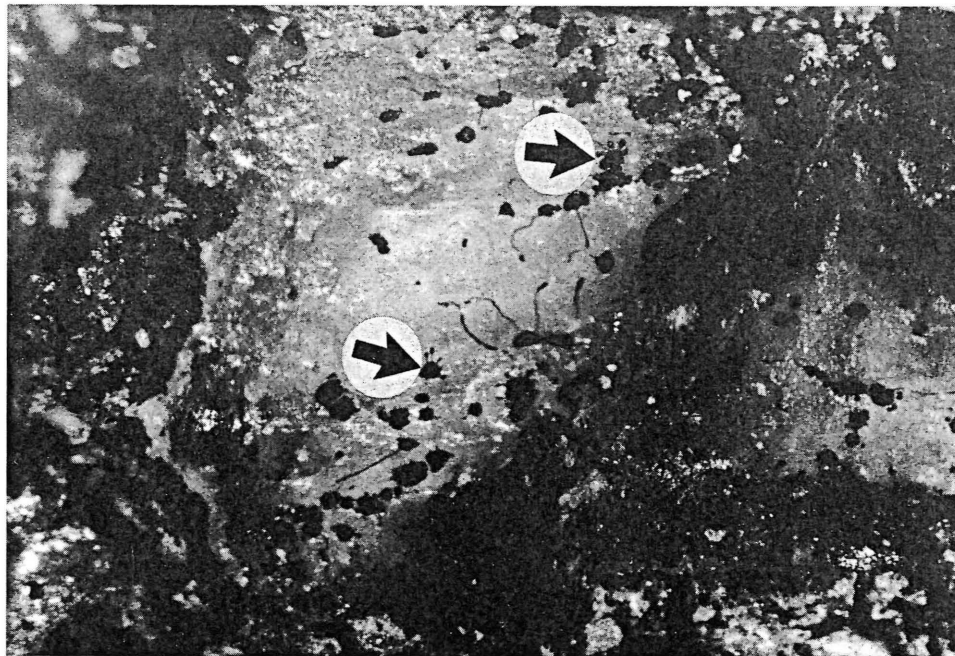


Figure 12: Surface view of quartz pebble showing numerous thalli of a microfungal *Lichenothelia* species (arrows).

terms of their supply of fog-water and condensing dew. Kappen (1985) found that porous sandstone dries out quickly on the exterior, but that inside the rock the relative humidity remained high for several days, thus prolonging the periods of metabolic activity of lithobiontic lichens. In an analogous way, the chasmoendolithic lichen may benefit from the availability of water as a result of the retardation of water loss through evaporation and under the cooler conditions which presumably prevail within the quartz. This will result in a prolongation of the physiologically active state of the lichen, especially during the early morning after dewfall or a fog incident of the previous night.

Apart from the aspects mentioned above, the major portion of the thallus of a chasmoendolithic lichen might experience fewer temperature extremes, due to the comparably higher albedo (with resulting reflectance of incoming short-wave radiation) and heat exchange properties of the quartz colonized by the lichen. The lag between maximum insolation and maximum temperature within quartz comparable to findings by Friedmann (1980) in granites in the Sonoran Desert Mexico, may play an important role in the prolongation of the physiologically active state of the chasmoendolithic *Lecidea* species.

Compared with epilithic lichens, the thallus of the chasmoendolithic *Lecidea* species is less exposed to the negative effects of wind such as evaporative water loss and abra-

sion of the thallus surface. The first mentioned phenomenon holds obvious advantages to the chasmoendolithic *Lecidea* species.

Thalli of the chasmoendolithic *Lecidea* species occur in microhabitats elevated above the surrounding soil surface (boundary layer), depending on the size of the quartz pebble or rock. Such microhabitats will differ from habitats adjacent to the soil surface in terms of light-, wind-, temperature- and water regimes (Kershaw, 1985).

A lichen thallus always contains one or more primary producers (species of green algae or cyanobacteria) and light is therefore one of the major features which influence the growth and morphology of chasmoendolithic lichen species. As a consequence only rock types that are translucent to some extent are colonizable by chasmoendolithic lichens. The steep light intensity gradient within the upper portion of the rock (Vogel, 1955; Friedmann, 1980) causes sharply delimited zones which in turn influence the internal morphology of the colonizing lichen.

According to Friedmann (1971) the outside environment in deserts is "hostile" to algal growth. Free living algae on the surface of rocks in desert regions are to date unknown (Friedmann, 1971). The reason they are unable to survive is probably due to the attainment of intolerably high levels of environmental factors such as irradiation and drought on the surface of desert rock (Friedmann, 1971). In the lichen symbiosis, the cortex protects the photobiont layer against the damaging effects of intolerable levels of irradiation, due to anatomical modifications of the layer and other features such as the presence of pigments. The photobiont layer in the chas-

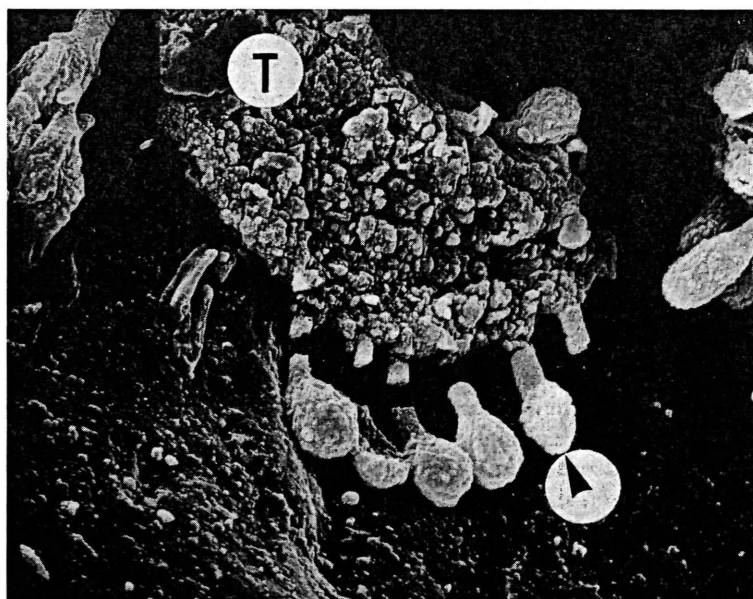


Figure 13: SEM micrograph of a thallus (T) of a species of *Lichenothelia* with stalked macroconidia. Arrowhead = stalked macroconidium.

moendolithic *Lecidea* species is, depending on its locality, protected from harmful radiation either by the pigmented cortex or by the quartz substrate which surrounds the lichen thallus. The protective and some of the physiological functions normally associated with the cortex of epilithic growth forms, are in chasmoendolithic lichens performed by the substrate in which the lichen grows. The protective role substrates play in lithobiontic habitats was recently shown by Büdel (1987). He determined that 2-5% of the irradiation on the surface of Clarens sandstone from the northern Transvaal, South Africa, reached the cyanobacterial layer which grew 1,5 - 2 mm below the surface of the rock. He found that these figures correspond well with the relative amounts of transmitted light in thalli of *Peltula euploca* which were 3,4% in wet thalli and 6,8% in dry thalli.

Euendolithic lichens from the Negev Desert have much higher maximal rates of net photosynthesis (per surface area) than cryptoendolithic lichens. Epilithic lichens on the other hand have maximal rates of net photosynthesis which are much higher than either of the above mentioned growth forms (Lange *et al.*, 1970). Kappen & Friedmann (1983a) showed that dry organic matter production by endolithic organisms in Antarctica is very low. They measured maximum rates of photosynthesis fewer than 0,1 mg CO₂/mg Chlorophyll·h in cryptoendolithic lichens. Although no such data exist on endolithic microorganisms of the Namib Desert, it is unlikely that dry matter production by endoliths in the Namib Desert will be dissimilar.

The standing biomass of endolithic microorganisms in the central Namib Desert is unknown. It may be large, considering the common occurrence and wide distribution of the endolithic lichen species and values reported by Friedmann (1980) for the Negev and Sonoran Deserts (37,5 to 185,0 gm⁻² of rock surface) and Friedmann *et al.* (1980) for Antarctica (32,25 to 176,75 gm⁻² of rock surface).

During the investigation the first observation of a species representing the microfungus genus *Lichenothelia* D. Hawksw. emend. in SWA/Namibia was made. A member of the genus (Figs. 12 & 13) was observed growing alongside the chasmoendolithic *Lecidea* species and on the surface of the quartz.

CONCLUSION

Plants and animals which exist in the Namib Desert are exposed to extreme fluctuations in terms of environmental conditions. Exploitation of favourable microclimates within the desert ecosystem is, therefore, essential to the existence of organisms living under such conditions. The organisms achieve this by either retreating or escaping (as the chasmoendolithic *Lecidea* does), from the harshness of the desert environment. The widespread occurrence and successful existence of endolithic lichens in the central Namib Desert underscores the advantages these organisms may gain from the endolithic niche, in combination with morphological modifications, because "the endolithic environment is an integral microscopic world upon which outside conditions have only a limited influence" (Friedmann, 1980). The success of these organisms in the central Namib Desert is aptly summarized by the words of Louw & Seely (1982), "most plants and animals survive in the desert because they do not

live in the desert?" Apart from successfully exploiting a seemingly favourable micro-habitat, the chasmoendolithic *Lecidea* species during colonization of quartz undoubtedly contributes to the weathering processes in the Namib Desert.

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