Endolithic Microorganisms in the Antarctic Cold Desert

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A report published in 1976 (*1*) describing endolithic cyanobacteria in rocks of the dry valleys of southern Victoria Land, Antarctica, was based on the examination of a single rock sample. Fieldwork during the past five austral summers (*2*) has revealed that a variety of microorganisms live under the surface of rocks in this area. Far from being of isolated occurrence, they colonize extended areas and produce considerable biomass. Sufficient information has now been collected that it is possible to give a comprehensive picture of this peculiar microbial ecosystem.

Summary. In the frigid desert of the Antarctic dry valleys there are no visible life forms on the surface of the soil or rocks. Yet in certain rock types a narrow subsurface zone has a favorable microclimate and is colonized by microorganisms. Dominant are lichens of unusual organization. They survive not by physiological adaptation to lower temperatures, but by changing their mode of growth, being able to grow between the crystals of porous rocks. Their activity results in mobilization of iron compounds and in rock weathering with a characteristic pattern of exfoliation. This simple ecosystem lacks both higher consumers and predators.

The Antarctic Cold Desert

The climate of the Antarctic continent is arid. This is especially true for the ice-free "oases" where dry katabatic (downslope) winds descending from the Antarctic ice plateau create true desert conditions and where extensive areas of rock and soil are without snow or ice cover. The dry valleys of southern Victoria Land are probably the largest and best known of these oases (Fig. 1). They cover an area of about 5000 square kilometers and lie between 160° and 164°E, and 76°30′ and 78°30′S. In the past, glaciers gouged out deep valleys of predominantly east-west orientation and subsequent glacial flow was cut off by the Transantarctic Mountains (*3*).

On the valley floors there are several lakes, most of them frozen, and during the austral summer, meltstreams (rivers) appear. In the mountains, where several peaks are in the range of 2000 to 2400 meters in altitude, the landscape is similar to a typical rocky desert (Fig. 2). In this article I consider only the high altitude (above approximately 1000 meters) desert areas of the dry valleys and exclude those parts which are affected by renewable sources of liquid water (meltstreams and lakes).

Air temperature ranges mostly between −15° and 0°C in the summer and it probably drops to near −60°C in the winter (*4*). Relative humidity ranged from 16 to 75 percent during five successive austral summer seasons (1976–1981) (*5, 6*). Information about the infrequent snowfall is scarce; reports (*7*) indicate that snow in the dry valleys mostly sublimes without melting or is blown away by winds. This we could confirm only partly, as on several occasions we observed melting snow as well as fog (*5, 6, 8*).

Life in the Antarctic Cold Desert

In this frigid desert there is no visible sign of plant or animal life; even epilithic crustose lichens, predominant in the maritime regions of Antarctica, are absent or very rare. Although numerous microorganisms have been isolated from dry valley soils (*9*), critical studies indicate that most if not all of these isolates are derived from atmospheric contaminants carried in by winds (*10*) and that they survive in frozen soil without actively growing. The occurrence of sterile soils has also been reported by several investigators (*10*), but this has been questioned by others (*11*). Although there is evidence that indigenous microorganisms exist in dry valley soils (*11*) their numbers appear to be very low.

The principal habitat for life in the dry valley desert is a narrow zone under the surface of rocks colonized by endolithic microorganisms. In the dry valleys, two types of endolithic organisms occur (*12*): chasmoendoliths living in rock fissures and cracks, and cryptoendoliths inhabiting structural cavities of porous rocks. As these organisms do not actively penetrate the substrate by solubilization, only those rocks which either have a porous structure or are weathered and permeated by fissures are colonized. Because endolithic microbial communities have a photosynthetic primary producer, only translucent rocks are suitable substrates. In the area of the dry valleys, such substrates are weathered Beacon sandstone (orthoquartzite), granite, granodiorite, and Koettlitz marble. These rocks are frequently colonized by microorganisms; dark and nonporous volcanic rocks such as Ferrar dolerite are rarely so.

Cryptoendolithic cyanobacteria. These blue-green algae, which occur under the surface of sandstone rocks (Fig. 3a), were described previously (*1*). Subsequent fieldwork, however, showed that such cyanobacterial communities are rather infrequent in the dry valley area. Several strains of these cyanobacteria were isolated in culture and identified as species of *Chroococcidiopsis* (or a related genus; the taxonomy of this group is unclear). The cyanobacteria in the rock are accompanied by unidentified colorless bacteria.

Cryptoendolithic lichens. The predominant rock-colonizing organisms are cryptoendolithic lichens in sandstones. A typical growth shows an upper black zone about 1 millimeter thick, then a white zone about 2 to 4 millimeters thick, and below this a green zone, the lower limit of which is often indistinct (Fig. 4). All zones are produced by filamentous fungi and unicellular green algae (Chlorophyceae) which together form a symbiotic lichen association (*13*). The colored zones superficially resemble the layers found in cross sections of many heteromerous lichens (*14*), and such a differentiation is an indication that the zones are parts of an organized thallus. However, these cryptoendolithic lichens represent an entirely different type of organization and morphology. In "typical" thalloid

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Fig. 1 (top). Ice-free areas in central portion of the dry valleys of southern Victoria Land, Antarctica. Stippled and solid areas indicate, respectively, ice-free areas under and over 1000 meters in altitude.

Fig. 2 (middle). Landscape in the high desert areas of the dry valleys; University Valley, 77°52′S, 160°39′E, 1650 meters in altitude. The sandstone cliffs are colonized by cryptoendolithic lichens.

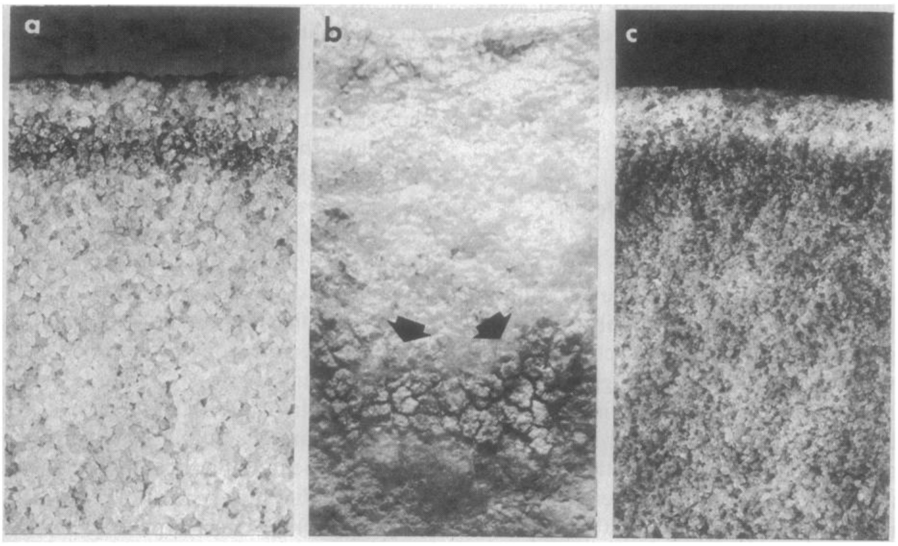

Fig. 3 (bottom). Types of endolithic microbial growths in sandstone from the dry valleys of southern Victoria Land. Fractured rock surfaces, ×4. (a) Cryptoendolithic cyanobacteria, forming a dark green to brown zone; University Valley. (b) Chasmoendolithic lichen (arrows) in fissure of silicified sandstone; Tyrol Valley, 77°35′S, 160°38′E, 1600 meters in altitude. (c) Cryptoendolithic lichen in iron-rich sandstone; University Valley. The lichen zone below the thin upper crust is bleached white, whereas the zone underneath, rich in iron compounds, appears darker than the bedrock below. The chemical analysis of the different layers of this specimen is given in Table 1.

lichens the mycobiont filaments form a coherent pseudotissue termed plectenchyma. In cryptoendolithic lichens, in contrast, loose filaments and cell clusters grow between and around the crystals of the rock substrate so that the lichen is embedded in the rock matrix, covered by the hard surface crust (*15*).

A diagrammatic illustration of a cryptoendolithic lichen is shown in Fig. 5A. The upper black zone is formed by dark brownish, grayish, or greenish masses of fungal (mycobiont) hyphae which, in turn, enclose groups of algal (phycobiont) cells. The hyphae often form small spherical bodies (Fig. 6, a and b) which resemble an early stage in the laboratory synthesis of fruticose lichens described as presquamules (*16*). Several of these presquamule-like spherical bodies can be matted together to form larger bodies. The dark pigmentation of the mycobiont in the black zone may be an adaptation to the environment: it absorbs light, thereby increasing the temperature (*5*, *17*).

In the white zone, colorless mycobiont filaments form a loose woolly web around crystals of the rock substrate. Phycobionts are sparse in this zone. In the green zone, by contrast, algal cells abound (Fig. 6, c and d). Functionally, the green zone resembles the phycobiont layer of heteromerous lichens, although the green zone is at the bottom (and thus farthest away from light), whereas in most other lichens the phycobiont layer is close to the surface (*18*). Below the green zone, colorless fungal hyphae often penetrate the rock substrate several millimeters further. In rocks where iron solubilization takes place in the lichen zone (as described below), these colorless hyphae are covered with precipitated iron compounds (probably hematite or goethite, or both).

On the cellular level, the relationship between the algal and fungal components follows the typical pattern of a lichen association. The mycobiont hyphae establish contact with the phycobiont cells by forming appressoria (hyphae surrounding the phycobiont, as shown in Fig. 7b) or haustoria (penetrating the phycobiont cells, as shown in Fig. 7, a and e). In the mycobiont cytoplasm, concentric bodies (Fig. 7c) are frequent. The function of these organelles is unknown, yet they are often regarded as characteristic of mycobionts (*19*). A further feature indicative of a lichen association is the production of lichen substances (*20*). The presence of norstictic acid, gyrophoric acid, and several unidentified substances was revealed by thin-layer chromatography analyses of lichen samples (*21*).

In cryptoendolithic lichens, the association of the mycobiont and phycobiont appears to be less stable than in plectenchymatous lichens. Algae were occasionally observed to grow out of the lichen association and to form nonlichenized algal masses (Fig. 6g) or, less frequently, hyphae were seen with no apparent connection to algae (Fig. 6h). There is also a certain variability in morphology. Although the vertical sequence of the black, white, and green zones is generally constant, any one or two of these zones may be absent. There is some indication that this variability is, at least in part, controlled by the environment. Thus, in places of low light intensity, such as the lower surface of overhanging rocks, the cryptoendolithic lichen growth may consist only of the green zone; in highly irradiated areas only the black zone may be present.

The life history of cryptoendolithic lichens is affected by a peculiar form of exfoliative weathering of the substrate (Figs. 5B, 8b, and 9) which, in turn, is a result of the activity of the organisms in the rock. The lichens thus exposed mostly dry out, crumble, and disperse. Some fragments possibly serve the vegetative propagation of the lichen, while the rest probably fall to the soil (*22*). Yet in certain circumstances, when microclimatic conditions create an exceptionally mild and favorable environment, the exposed cryptoendolithic lichen continues to grow on the surface of the rock. Such growths are limited to very small areas. This change to epilithic growth form is accompanied by changes in the morphology of the lichen as shown in Fig. 5A. Instead of being composed of free filaments characteristic of cryptoendolithic growth, the epilithic lichen forms a "typical" plectenchymatous thallus (Fig. 6e) with a defined external morphology. It

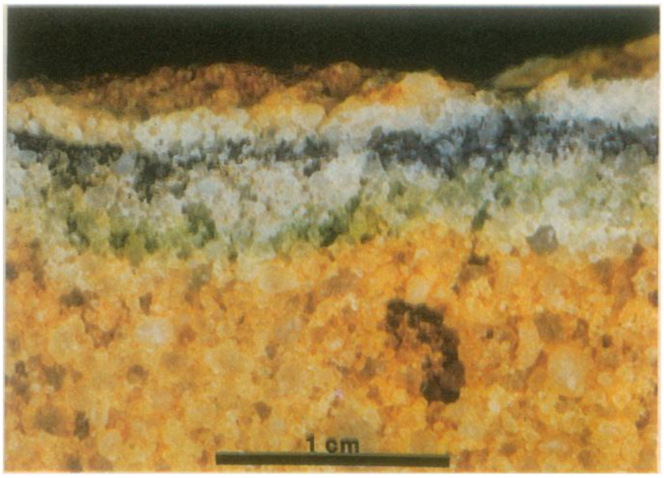

Fig. 4. Fractured sandstone, showing black, white, and green zones of cryptoendolithic lichen under the surface. Linnaeus Terrace, Asgard Range.

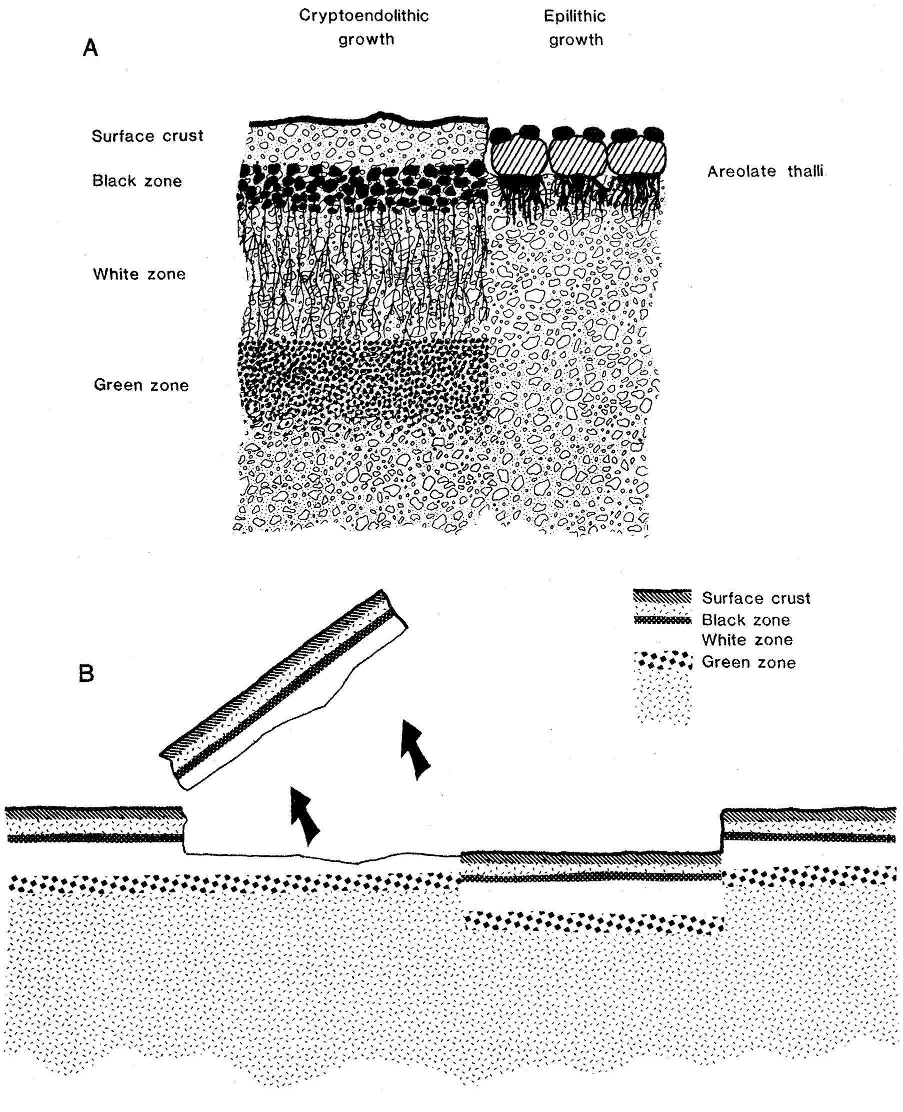

Fig. 5. Diagrams of lichen in sandstone. (A) Structure of cryptoendolithic growth and relation to epilithic, areolate growth form. The areolate thalli appear in protected areas after loss of the surface crust by biogenous weathering. (B) Exfoliative rock weathering, showing (from left to right) initial level of lichen growth; exfoliation of surface crust due to biological activity; site of earlier exfoliation with the lichen growing deeper into the rock substrate, and formation of new surface crust; and portion of old surface crust at initial level of lichen growth.

Table 1. Concentrations of metals at different levels in a sample of Beacon sandstone colonized by cryptoendolithic lichen and shown in Fig. 3c. The data are given as percentages of the weight of the sample (*27*).

Zone	Na_2O	K_2O	MgO	CaO	MnO	FeO	ZnO	PbO
Upper rock crust	0.03	0.09	0.02	0.06	0.005	0.60	0.00	0.0003
Leached lichen zone	0.00	0.00	0.00	0.00	0.000	0.01	0.00	0.0000
Dark brown zone below leached lichen zone	0.00	0.01	0.00	0.00	0.000	0.44	0.00	0.0010
Bedrock	0.00	0.05	0.01	0.00	0.001	0.18	0.00	0.0003

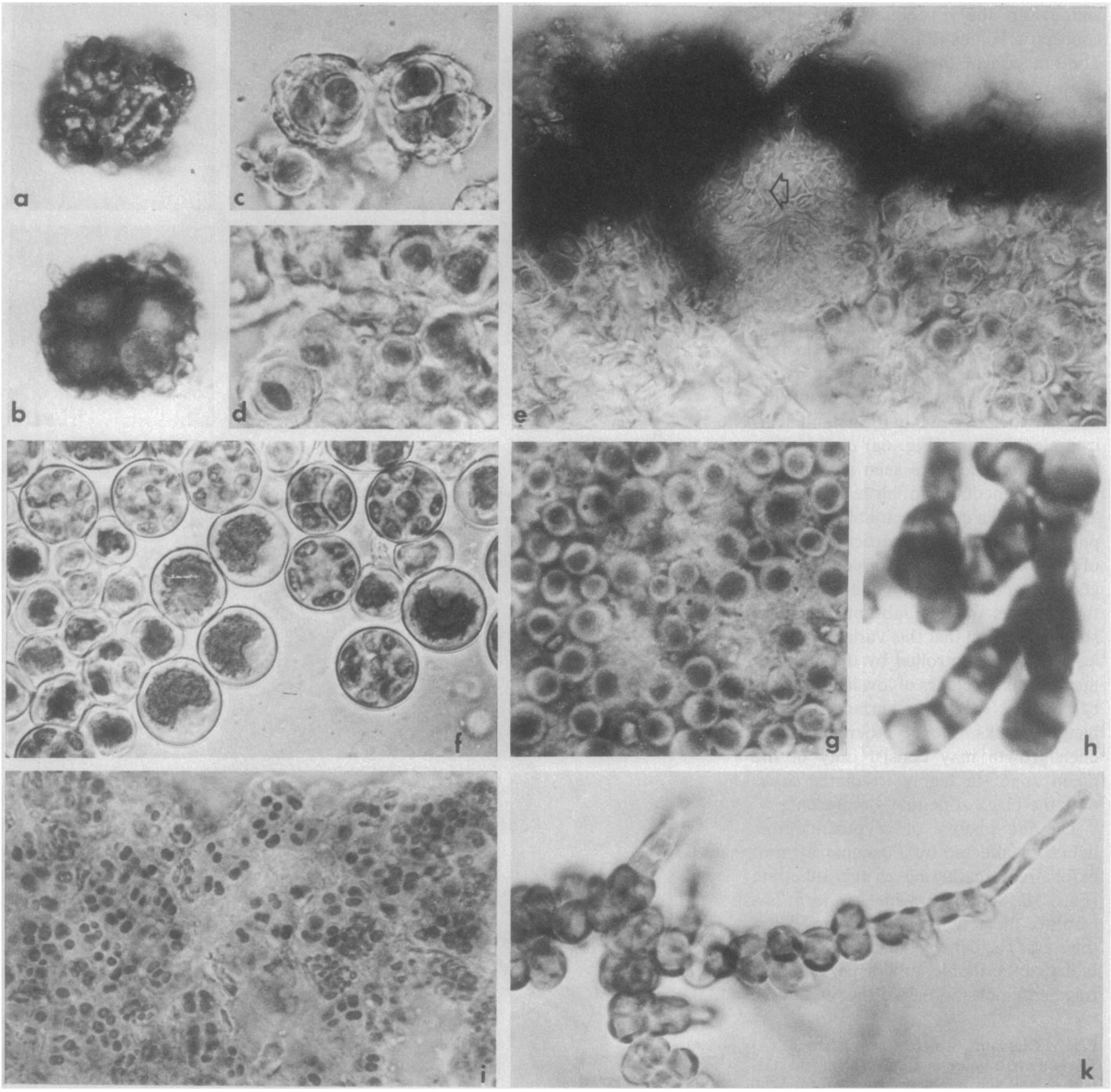

Fig. 6. Endolithic microorganisms of the dry valleys in the light microscope. (a–e) Cryptoendolithic lichens in sandstone. (a) Presquamule-like bodies from the black zone in surface view, showing mycobiont filaments. (b) The same photographed at a lower level (optical section), showing phycobiont cells in the center. (c) Phycobiont cells (*Trebouxia* sp.) and mycobiont filaments from the green zone (compare with Fig. 7b). (d) A different phycobiont with mycobiont filaments from the green zone. (e) Section of epilithic areolate thallus, showing dense plectenchymatous structure and a pycnidium with pycnospores (arrow). (f) *Trebouxia* sp., a phycobiont growing in culture. (g) Free-living, nonlichenized alga, presumably a phycobiont that became free from the lichen association, growing in the rock substrate. (h) Fungus filaments, presumably a mycobiont that became free from the lichen association. (i) Chasmoendolithic cyanobacteria in granite. (k) *Heterococcus* sp. (Xanthophyceae), chasmoendolithic in weathered marble. (a–d) and (f–k), ×1000; (e), ×500.

now appears as a crustose lichen with an areolate structure (composed of numerous small units, the areolas). These conditions are illustrated in Fig. 10. When viewed stereoscopically, it shows the lichen thallus "growing out" from under the upper rock crust, a part of which has been lost through exfoliation.

Less porous sandstones are less suitable for cryptoendolithic colonization. Here the lichens may grow in vertical fissures of the rock, becoming chasmoendolithic. In narrow, microscopic fissures their morphology is similar to the cryptoendolithic form, that is, the lichens form no plectenchyma, but in wider fissures a plectenchymatous areolate thallus may appear (Fig. 3b).

Cryptoendolithic lichens generally do not have sexual reproductive structures. Only when they become epilithic or chasmoendolithic do they form apothecia or pycnidia (*23*) (Fig. 6e). Lichen taxonomy is based mostly on these reproductive structures and on this basis three genera were identified, *Buellia*, *Lecidea*, and *Acarospora* (*21*). Although these genera belong to different families, they show a remarkable morphological similarity in their cryptoendolithic growth form. The genera are common in other areas of the continent. The Antarctic lichen flora of Dodge (*24*) lists 68 species of *Buellia*, 34 of *Lecidea*, and 13 of *Acarospora*, out of a total of 434 Antarctic species belonging to 90 genera. Cryptoendolithic lichens may be growth forms of epilithic species or perhaps exist only as cryptoendoliths, having been permanently adapted to their environment.

In several samples, the phycobiont was the green alga *Trebouxia* (Chlorococcales), a common lichen phycobiont (Fig. 6c). Figure 6f shows a strain of *Trebouxia* isolated in culture. Other unicellular green algae, among them a yet unidentified new genus (*25*), also participate in the cryptoendolithic lichen association (Fig. 6d).

Cryptoendolithic lichens are regularly accompanied by unidentified colorless bacteria. They form microscopic colonies visible with both light and electron microscope (Fig. 7f) and presumably function as decomposers.

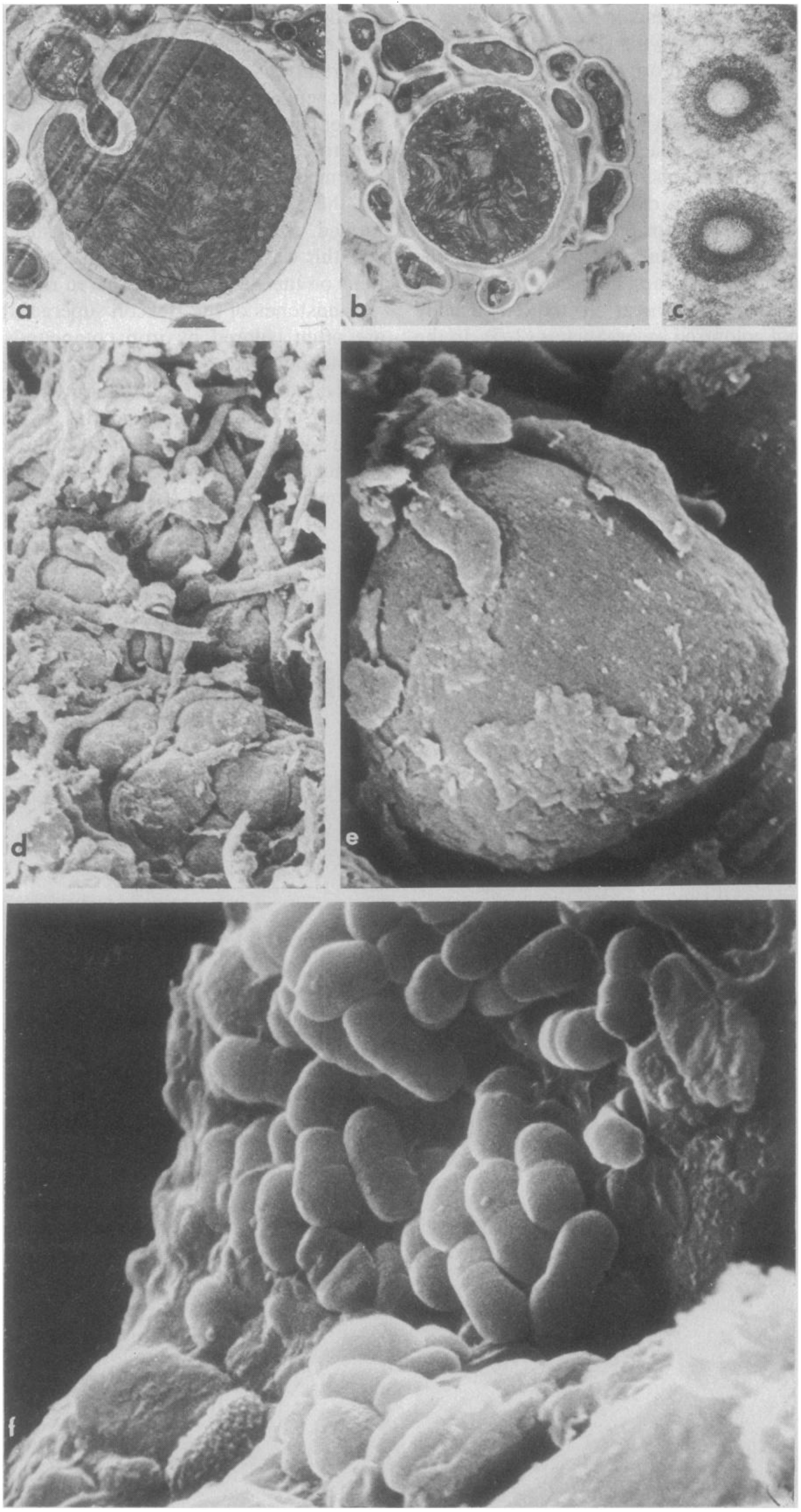

Fig. 7. Endolithic microorganisms of the dry valleys in the electron microscope. (a–c) Cryptoendolithic lichen in the transmission electron microscope. (a) Phycobiont (*Trebouxia*) cell penetrated by mycobiont haustorium [compare with (e)], ×3000. (b) Phycobiont cell with appressoria (the fungus component does not penetrate the alga) (compare with Fig. 6c), ×3000. (c) Concentric bodies from the mycobiont shown in (b), ×75,000. (d and e) Cryptoendolithic lichen in the scanning electron microscope. (d) Phycobiont cells and mycobiont filaments growing in the airspaces of the rock, without forming a dense plectenchyma, ×1000. (e) Phycobiont cell from specimen shown in (d), with fungus haustorium [compare with (a)], ×5000. (f) Rod-shaped bacteria accompanying cryptoendolithic lichen, attached to the surface of the rock substrate, ×20,000.

Biological Rock Weathering and Mineral Mobilization

In sandstone, the activity of cryptoendolithic lichens results in a characteristic exfoliative weathering pattern. The rock boulder in Fig. 8a shows on the left side such biogenous weathering (Fig. 8b), whereas the uncolonized right side is weathered by wind (Fig. 8c). The difference is due to orientation: rock surfaces with northern exposure receive direct solar radiation, causing the rock temperature to rise; this "warm face" is suitable for lichen colonization. Surfaces with southern exposure receive less insolation and are more exposed to katabatic winds. On such a "cold face" the temperature does not rise much above that of the ambient air and it is usually not colonized by organisms (*2, 5*). In the narrow University Valley (Beacon Valley area), the warm face of sandstone boulders is that facing the opening of the valley (northwest), whereas the opposite cold face is in mountain shadow and receives the prevailing southeast winds.

The weathering process itself is illustrated in Fig. 5B. The cementing substance between the sandstone grains is apparently solubilized (*26*) at the level of the lichen, and the upper rock crust peels off, exposing the lichen. Hyphae then penetrate deeper and a new lichen zone is formed at the appropriate depth, while on the surface a new rock crust is formed. Subsequent layers are "sliced off" this way, resulting in steplike elevations on the surface of weathered rocks.

Sandstones of the Beacon supergroup are often colored by iron compounds. Cryptoendolithic lichens mobilize these compounds; as a result, the rock is leached of iron-bearing minerals in the white zone, whereas the thin crust above the lichen and the rock substrate a few millimeters below it appear darker because of iron deposition at these levels. This in turn indicates that iron compounds mobilized by the lichen are being carried by water in two directions: downward when snow melts on the surface and upward when capillary water rises as a result of evaporation. An example of this is illustrated in Fig. 3c, and metal concentrations at different depths in the same sample are shown in Table 1 (*27*). Exfoliative weathering in such iron-rich dark sandstones may result in a colorful patchwork pattern of light brownish surface crust, and snow-white and dark reddish brown exposed rock (Fig. 9).

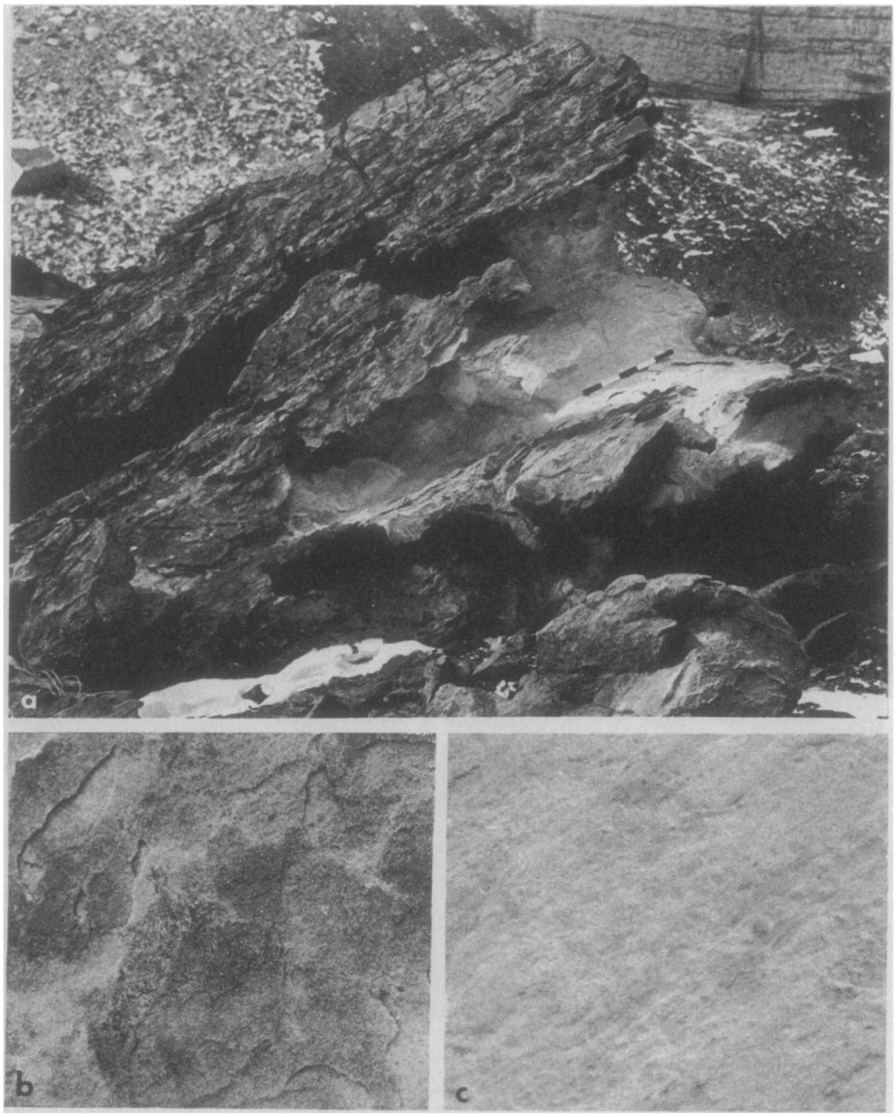

Fig. 8. Biogenous rock weathering in Beacon sandstone. (a) Boulder in University Valley. "Warm" face (left) exposed to the northwest is colonized by cryptoendolithic lichens and shows exfoliating weathering. The dark color is due to iron compounds. "Cold" face (right) exposed to the southeast is not colonized by organisms and is weathered by wind action. The light color is that of the bedrock. Scale: 50 cm. (b) Biogenous exfoliating weathering on "warm" face of boulder exposed to the north. Linnaeus Terrace, ×0.25. (c) Aeolian weathering on "cold" face of the same boulder exposed to the south, ×0.25.

Chasmoendolithic Microorganisms

In granite and granodiorite, lichens or coccoid cyanobacteria may colonize cracks under the abiotically weathered rock crusts (*2*) (Fig. 6i). The chasmoendolithic lichens, when growing in the fine cracks of the rock substrate, do not form a plectenchyma. Yet, similar to cryptoendoliths, they can become epilithic and form areolate plectenchymatous fertile thalli that could be identified as *Buellia* or *Lecidea* (*21*). The phycobionts are unicellular green algae, mostly *Trebouxia*.

Dolerite, common in the dry valleys, is only rarely colonized by lichens (*23*). When it is so colonized, the lichens grow in wide vertical fissures, about 10 to 15 millimeters deep with the upper surface of the organisms fully exposed to sunlight. These conditions are illustrated in the stereoscopic photograph shown in Fig. 10. The lichen is a *Buellia* species with an areolate thallus and reproductive structures.

The coastal desert at Marble Point, near the frozen Ross Sea, is not a part of the high altitude desert of the dry valleys, but is mentioned here because of the chasmoendolithic growth that exists in the rocks (*2*). Elevation is about 20 to 60 meters above sea level and the climate is milder and more humid than in the mountainous areas. The outcrops of weathered Koettlitz marble are traversed by numerous microscopic cracks. They are heavily colonized by several (about 12 to 15) species of unicellular and filamentous green algae and cyanobacteria, accompanied by colonies of colorless bacteria; lichens or fungi seem to be absent. One of the characteristic algae (Fig. 6k) is a species of the xanthophycean genus *Heterococcus*, a soil alga of worldwide distribution (*28*).

Possibly similar growths of chasmoendolithic green algae and cyanobacteria have been found recently in two other

Antarctic coastal desert areas near David Station (Vestfold Hills, Princess Elizabeth Land) and near Mawson Station (MacRobertson Land) (*29*).

Adaptations to the Endolithic Microenvironment

The conspicuous absence of organisms on the rock surface is in contrast to the rich microbial zone a few millimeters below, raising the question of the possible causes for the abiotic conditions on the surface. In the cold desert of the dry valleys, the critical environmental factors are temperature and availability of water.

Melting snow is the main source of water. It is readily absorbed by the porous rocks, which act as a water reservoir. Probably the best indication of the availability of water is the relative humidity in the airspaces of rocks. It has been shown that lichens in general, and specifically Antarctic lichens, can take up water vapor from the air (*30, 31*), and it seems probable that cryptoendolithic forms can do the same. Following a snowfall on Linnaeus Terrace (Asgard Range) in December 1979, relative humidity in the rock airspaces remained above 80 percent for at least 5 days whereas in the atmosphere it repeatedly dropped below 20 percent (*5*). It is unlikely, however, that aridity alone would account for the absence of lichens on the rock surface: in hot deserts, rock surfaces are probably more arid and yet they are colonized by crustose lichens.

Temperature of the northern (warm) rock face may rise close to 20°C above the ambient, reaching at the level of the lichens 10°C or more. At the same time, the temperature of the surface is often several degrees lower, because of convection due to winds (*2, 32*). Yet, low temperature does not quite explain the absence of lichens on the surface. Lichens are known to be able to tolerate extreme cold and even to photosynthesize at temperatures as low as −24°C (*33–35*), which is below the usual range of summer temperatures in the dry valleys.

Probably the most important single factor responsible for the abiotic rock surface is the rapid fluctuation of temperature due to gusty winds, a frequent weather pattern in the dry valleys. In the prevailing temperature range of the summer, these fluctuations often occur around 0°C, resulting in a sequence of rapid freezing and thawing on the surface. For example, on 25 December 1980, during a period of 42 minutes starting at 0830 hours, temperature on the rock surface fluctuated between −1.8° and +5.9°C with an amplitude of 7.7°C, and moved across 0°C no less than 14 times. During the same period, temperatures in the lichen zone (3 millimeters below the surface) were at all times above 0°C, ranging from 1.7° to 6.1°C with an amplitude of 4.4°C (*32*).

The extreme conditions on the rock surface apparently create a barrier to colonization that cannot be overcome by physiological adaptations. It is therefore not surprising that, according to CO_2 exchange measurements in the laboratory, cryptoendolithic lichens of the dry valleys are not better adapted to low temperatures than crustose forms from the maritime Antarctic region of northern Victoria Land. In both groups, the lower limits of net photosynthesis were between about −8° and about −6°C, whereas optimum temperatures ranged from about 1° to about 9°C (*31, 36*).

What special adaptations do cryptoendolithic lichens possess that are different from those of other Antarctic forms? The cryptoendolithic niche provides a comparatively mild environment, but it is accessible only to organisms that are able to penetrate the narrow airspace system of the porous rock. Unicellular organisms like bacteria are able to do this, but lichens with a plectenchymatous structure have to undergo fundamental changes in their pattern of growth

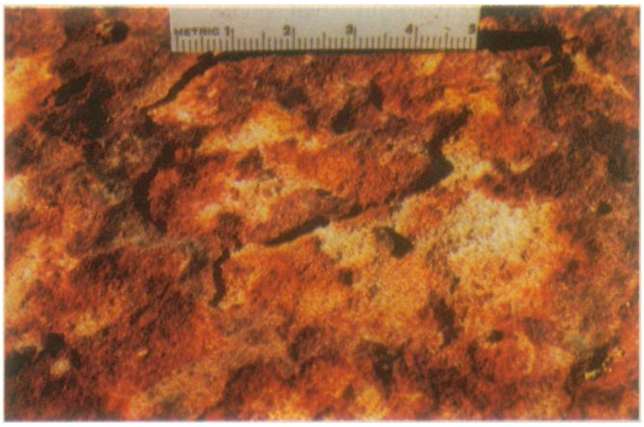

Fig. 9. Exfoliative weathering in sandstone with high iron content, showing patchwork-like pattern of white, straw-colored, and dark brown areas. Linnaeus Terrace.

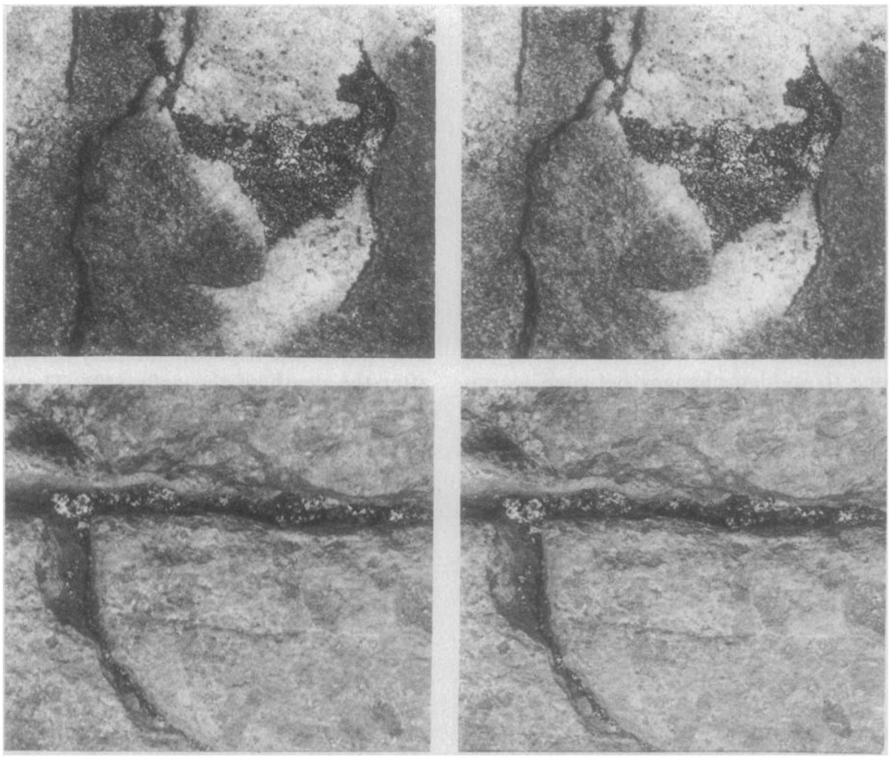

Fig. 10. Stereophotographs of lichens in dry valley rocks, natural size. (Top) Epilithic areolate stage of cryptoendolithic *Buellia* species formed where surface crust was lost as a result of exfoliation (see Fig. 5); Linnaeus Terrace. (Bottom) Chasmoendolithic *Buellia* species in fissure of dolerite rock. Top of Finger Mountain, 77°45′S, 160°37′E, 1900 meters in altitude.

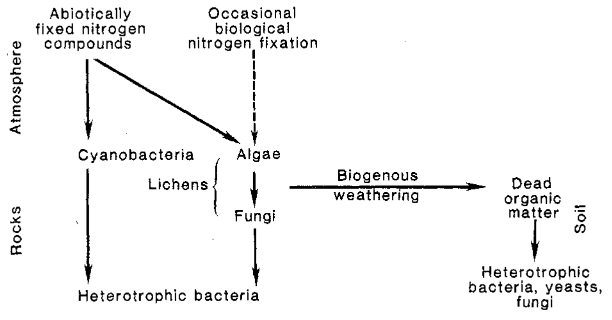

Fig. 11. Principal pathways of nutrient flux.

in order to colonize such a substrate. The unique adaptive achievement of Antarctic cryptoendolithic lichens is the ability of the mycobiont to change its growth from plectenchymatous to filamentous while still maintaining thallus organization with defined layers, and to revert to plectenchymatous when conditions so permit.

In the rapidly changing weather of the dry valley desert, microbial metabolic activity is limited to periods when the appropriate combination of temperature and humidity is present. At other times, extreme cold or aridity, or both, prevail. Hence, these organisms need to respond to frequent changes in the environment by rapidly switching their metabolic activities on and off, a strategy typical of poikilohydric organisms such as lichens (*35*). In addition, Antarctic cryptoendolithic types, like other lichens, also have to cope with the particular problems connected with drought survival and rewetting (*37*).

These conditions may significantly limit the length of time during which photosynthesis is possible, but do not necessarily impose a severe physiological stress on the organisms. During periods of inactivity they are frozen, a condition that many microorganisms, quite especially lichens, endure without damage (*31, 34, 38*). In contrast, endolithic organisms in hot deserts are subject to much more severe environmental stress due to sudden changes between warm-humid "favorable" and hot-dry "unfavorable" conditions. As discussed elsewhere (*39*), this is apparently the reason for the absence of eukaryotic organisms in the endolithic microbial community in hot desert rocks.

Nutrients, Ecosystem, and Biomass

The inorganic nutrients required by endolithic microorganisms are probably available in the rock substrate (Table 1). Nitrates and ammonium compounds are generally present in the upper few centimeters of Antarctic rocks (*40*). Nitrogenous compounds, probably abiotically fixed in the upper atmosphere, are conveyed to the rock by snow or dry fallout. This phenomenon may explain why nitrogen-fixing microorganisms are rare in these endolithic microbial communities. In the few cases when potential nitrogen fixers are present, nitrogen fixation may be inhibited by the presence of nitrogen compounds (*40*). Hence, the ability to fix atmospheric nitrogen does not seem to be of selective advantage in this environment.

The ecosystem of the dry valley desert is simple. Cyanobacteria and phycobionts are the primary producers; mycobionts may be regarded as consumers and colorless bacteria as decomposers. Secondary consumers and predators are absent, and in this respect the ecosystem resembles that of the dry valley lakes (*41*). The principal pathways of nutrient flux are shown in Fig. 11.

The biomass of the endolithic microbial community was estimated on the bases of adenosine triphosphate, organic nitrogen, and chlorophyll *a* determinations (*42*). Estimates of total organic matter in Beacon sandstone colonized by cryptoendolithic lichens ranged from 46 to 177 grams per square meter of rock surface; in that colonized by cyanobacteria the values were 32 to 59 grams per square meter. In the Antarctic climate, decomposition is extremely slow and even adenosine triphosphate may persist after the death of the cells (*42*). These values include both living and dead organic matter and the comparatively large endolithic biomass is not indicative of high productivity.

The Dry Valleys:
Terrestrial Model for Mars?

Since 1970, the Antarctic dry valleys have been considered the closest terrestrial analog of the martian environment (*10, 11, 43*), and hypotheses about the possibility of life on Mars were based on this comparison. With more information available about the dry valley ecosystem, it may now be possible to reexamine the validity of such assumptions.

The cryptoendolithic microorganisms of the Antarctic cold desert survive in an inhospitable environment without actually adapting to its extremes. Within a largely hostile macroclimate, they find refuge in a microscopic niche where conditions suitable for life exist. It also appears that, in the dry valleys, the endolithic niche provides a more effective shelter from the outside environment than do soils.

These endolithic microorganisms cannot be regarded as examples of "primitive" life. On the contrary, they are highly adapted to a special set of environmental conditions. Such an endolithic community may have evolved when conditions for life deteriorated (for example, because of glaciation) and organisms retreated into the protected niche provided by the inside of porous rocks.

References and Notes

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13. Symbiotic lichen associations are traditionally treated as "species," although they actually contain two different organisms, a fungus (termed mycobiont) and an alga (phycobiont).
14. Heteromerous lichens form distinct stratified layers of cortex, green phycobiont layer, and colorless medulla, whereas in homoeomerous lichens there is no such differentiation.
15. Cryptoendolithic lichens are fundamentally different from the "endolithic lichens" which occur worldwide on rock substrates. These endolithic lichens grow from the surface into the rock substrate. A more or less well developed portion of the vegetative thallus (or at least reproductive structures) remains on the surface while part of the lichen penetrates the substrate either by active dissolution of the rock substance [H. W. Doppelbaur, *Planta* **53**, 246 (1959)] or by growing between crystals of weathering rock. If one follows the terminology proposed by Golubic *et al.* (*12*), these lichens should be referred to as euendolithic.
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Directly Transmitted Infectious Diseases: Control by Vaccination

Roy M. Anderson and Robert M. May

Observed patterns of human mortality have changed in Europe over the past three centuries, with life expectancy increasing from about 25 to 30 years in 1700 to about 70 to 75 years in 1970 (*1*, *2*). This improvement comes mainly from a decline in deaths from infectious disease; although the phenomenon is still not fully understood, it appears that higher standards of hygiene and nutrition, possibly combined with changes in the genetic structure of human and parasite populations, have acted concomitantly to decrease the pathogenicity of many common disease agents (*1*).

In contrast with this decrease in mortality, the frequency and magnitude of epidemics of disease increased during the 18th and 19th centuries, principally as a result of changing social patterns and the growth of large centers of population in increasingly industrialized societies. The reversal of this trend during the present century is largely due to the development and widespread use of vaccines to immunize susceptible populations against various directly transmitted viral and bacterial diseases (*3*, *4*). Some notable achievements have occurred in the last 50 years. Smallpox has been eradicated worldwide (*5*), and the incidences of diphtheria and paralytic poliomyelitis have declined to very low levels in Europe and North America (*3*).

Many airborne infectious diseases, however, remain endemic throughout most of the developed world, despite the widespread use of vaccines. For example, Fig. 1 shows the history of measles and whooping cough in England and Wales from 1940 to 1979. These two infections remain a hazard to some children in Europe, and in underdeveloped regions of Africa and Asia, where malnutrition is rife, they are a significant threat to life (*6*).

A first step toward the successful control or eradication of a communicable disease is the development of a safe, effective, and cheap vaccine that provides lasting (ideally lifelong) protection. Once this has been done [as it has, for example, for measles (*3*, *6*)], important epidemiological questions remain to be answered. What proportion of the population must be immunized in order to eradicate the disease? What reduction in disease incidence is to be expected from a given age-specific vaccination schedule? What is the effect of vaccination on the average age at which individuals acquire infection, and on the time between epidemics (the "interepidemic period")? This article draws together theory and the extensive data that are available, particularly for measles and whooping cough in Britain, to suggest some answers to these and other, related questions; the answers involve knowledge both of the typical course of infection within an individual [such as the length of the latent period, and the duration of infectiousness (*7*)] and of the overall population biology of the disease agent and its host (*8*–*10*).

The mathematical literature dealing with the design of optimal vaccination programs has expanded rapidly (*11*–*13*). With some notable exceptions (*14*), these insights have had relatively little impact on public health policy. This may be due, in part, to the abstractly mathematical nature of much of this research, to its lack of contact with epidemiological data (*15*), and to the focus on short-term strategies to control isolated epidemics as opposed to long-term national or regional policies to control endemic diseases (*11*). One aim of our article is to

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