3.6 Cryptoendolithic Lichen and Cyanobacterial Communities of the Ross Desert, Antarctica

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Summary: Cryptoendolithic microbial communities in the Ross Desert (McMurdo Dry Valleys) are characterized on the basis of photosynthetic microorganisms and fungi. Two eukaryotic communities (the lichen-dominated and *Hemichloris* communities) and three cyanobacterial communities (the red *Gloeocapsa*, *Hormathonema-Gloeocapsa*, and *Chroococcidiopsis* communities) are described. Eleven coccoid, ohne pleurocapsoid, and five filamentous cyanobacteria occurring in these communities are characterized and illustrated. The moisture grade of the rock substrate seems to affect pH, formation of primary iron stain, and the distribution of microbial communities.

Zusammenfassung: Anhand von Photosynthese treibenden Mikroorganismen und Pilzen werden kryptoendolithische Mikrobengemeinschaften in der Ross Desert (McMurdo Dry Valleys) charakterisiert. Es werden zwei eukaryotische Gesellschaften (eine mit dominierenden Flechten und eine *Hemichloris*-Gesellschaft) und drei Cyanobakterien-Gesellschaften (rote *Gloeocapsa*-G., *Hormathonema-Gloeocapsa*-G. und *Chroococcidiopsis*-G.) beschrieben. Elf coccoide, eine pleurocapsoide und fünf fädige Cyanobakterien, die in diesen Gesellschaften vorkommen, werden genauer beschrieben und abgebildet. Der Wassergehalt im Felssubstrat scheint den pH-Wert, die Eisenpigmentierung des Gesteins und die Verteilung der mikrobiellen Gemeinschaften im Gestein zu beeinflussen.

1. INTRODUCTION

The cryptoendolithic microbial communities of the Ross Desert in the McMurdo Dry Valleys colonize sandstones of the Bacon supergroup. Since earlier reports (FRIEDMANN 1977, 1982), new evidence has accumulated about these communities and their complex structure. On the recently explored Battleship Promontory (76° 55' S, 160° 55' E) in the Convoy Range, communities were found that are dominated by cyanobacteria and lack lichens, free-living fungi, or eukaryotic algae. Most cyanobacteria in these communities appear to be new to science.

In this paper, we summarize available information on the principal microbial communities and give short descriptions of the cyanobacterial types. Up to this time, most of these cyanobacteria have not been successfully cultured. Their detailed characterizations and diagnoses will be published at a later date.

Information on geological aspects of the Beacon sandstone substrate has been recently summarized by WEED (1985), WEED & ACKERT (1986), FRIEDMANN & WEED (1987), and WEED & NORTON (in press). The geology of Battleship Promontory has been described by MIRSKY et al. (1965).

Perhaps the most conspicuous feature of the Ross Desert cryptoendolithic microbial communities is the vertical zonation present in all but a few cases. This vertical zonation correlates with the steep light gradient in the upper few millimeters of the rock (NIENOW et al. 1988). In most cases, there are two major zones that differ in color. In some communities, the upper and the lower zones may be further differentiated.

The principal types of sandstone-inhabiting cryptoendolithic communities of the Ross Desert are summarized in Table 1. Characterization is based on photosynthetic microorganisms and fungi, as these are the most conspicuous members of the communities. Some of the communities are dominated by eukaryotic organisms, whereas others seem to be formed entirely of prokaryotes. As information on heterotrophic bacteria is fragmentary, these could not be considered here. It should be kept in mind, however, that all communities contain diverse nonphotosynthetic bacteria.

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EUKARYOTIC COMMUNITIES		CYANOBACTERIAL COMMUNITIES		
Lichen-dominated community	*Hemichloris* community	Red *Gloeocapsa* community	*Hormathonema-Gloeocapsa* community	*Chroococcidiopsis* community
Lichen fungi (mycobionts)	***Hemichloris antarctica***	***Gloeocapsa* species 1**	***Hormathonema* sp. and/or**	***Chroococcidiopsis* sp.**
Parasymbiontic fungi (lichen parasites)		*Gloeocapsa* species 7	*Gloeocapsa* species 2	
Trebouxia spp.		*Gloeocapsa* species 2	*Gloeocapsa* species 3	
Pseudotrebouxia spp.		*Gloeocapsa* species 3	*Anabaena* species 1	
		Eucapsis sp.	*Anabaena* species 2	
		Microchaete sp.		
Hemichloris antarctica				
Gloeocapsa species 1			***Aphanocapsa* sp.**	
Chroococcidiopsis sp.		*Gloeocapsa* species 8	*Gloeocapsa* species 4	
Heterococcus endolithicus			*Gloeocapsa* species 5	
Stichococcus sp.			*Gloeocapsa* species 6	
Hyaline fungi			*Anabaena* species 3	
			Lyngbya sp.	

Tab. 1: Cryptoendolithic microbial communities in the Ross Desert. Characteristic organisms of the communities are printed in bold face.

2. ROSS DESERT CRYPTOENDOLITHIC MICROBIAL COMMUNITIES

2.1 *Eukaryotic Communities*
2.1.1 Lichen-dominated communities

The upper zone is formed by cryptoendolithic lichens (Fig. 1a, FRIEDMANN 1977, 1982). The taxonomy of these lichens is still somewhat uncertain. HALE (1987) described six lichen species (*Acarospora gwynnii* Dodge & Rudolph, *Buellia grisea* Dodge & Baker, *Carbonea capsulata* (Dodge & Baker) Hale, *Lecanora fuscobrunnea* Dodge & Baker, *Lecidea canariformis* Dodge & Baker, and *L. siplei* Dodge & Baker) that form apothecia on rocks colonized by cryptoendolithic lichens. These apothecia are generally rare in nature and occur only in proctected microhabitats, such as small depressions in rocks (FRIEDMANN et al. 1980). Connection between these epilithic apothecia and the cryptoendolithic growth form seems to be evident in many cases, but is uncertain in some. Thus, it is unclear whether all species described by Hale are connected to cryptoendolithic growth forms; some species may represent epilithic lichens that occur in protected microhabitats without forming cryptoendolithic stages. Several fungal strains have been isolated from the cryptoendolithic stages (AHMADJIAN & JACOBS 1987, KORIEM & FRIEDMANN unpubl., MINTER & FRIEDMANN unpubl.) that were shown by artificial lichen recognition experiments to function as mycobionts. No clear identification with the apothecial stages has been possible to date, and it is therefore possible that some of the cryptoendolithic mycobionts do not form apothecia. The phycobionts of the cryptoendolithic lichens belong to the genera *Trebouxia* and *Pseudotrebouxia* (ARCHIBALD et al. 1983, TSCHERMAK-WOESS & FRIEDMANN unpubl.). Several strains that seem to belong to different species have been isolated but are not yet taxonomically identified.

Within this upper (cryptoendolithic lichen) zone, there is a further differentiation into an upper black zone and a lower white zone. The black zone may be formed by two different structures: It may contain lichen soredia with pigmented phycobiont filaments described earlier as "presquamule-like bodies" (FRIEDMANN 1982). Alternatively, the black zone may contain non-lichen-forming pigmented fungi. Several of these dark-pigmented fungi, which do not form lichens in artificial resynthesis experiments (KORIEM & FRIEDMANN unpubl.), have been isolated in culture. They occur in association with the cryptoendolithic lichens and are probably parasymbionts (lichen parasites). The white zone, in contrast, appears to be formed only by lichens (i. e., contains no parasymbionts) and may also contain hyaline (colorless) soredia.

The lower zone of the lichen-dominated community (green zone) was thought earlier (FRIEDMANN 1982) to be part of the lichen. We now know that this is not the case. The characteristic organism of the lower zone is the

Fig. 1: Ross Desert cryptoendolithic communities and characteristic weathering patterns. a—e: Fractured sandstones colonized by cryptoendolithic communities. scale = 5 mm: a: Lichen-dominated community. Battleship Promontory, the absence of primary iron stain is somewhat unusual in this community; b: *Hormathonema-Gloeocapsa* community. Battleship Promontory; c: Red *Gloeocapsa* community. Linnaeus Terrace, with primary iron stain and leached zone; d: *Chroococcidiopsis* community, Tyrol Valley, sample A 303 collected by W. V. Vishniac; e: Transition between *Hormathonema-Gloeocapsa* community (left) and lichen-dominated community (right). Battleship Promontory, from a site similar to g; f—h: Exfoliative weathering patterns caused by cryptoendolithic colonization. scale = 10 cm: f: *Hormathonema-Gloeocapsa* community, moiré-like pattern of blackish lines; g: Lichen-dominated community, patchwork-like exfoliation pattern with brownish iron stain (above) and *Hormathonema-Gloeocapsa* comunity, exfoliation like f (below). rock outcrop on dolerite rubble; h: *Hormathonema-Gloeocapsa* community, exfoliation like f, sandstone clast on dolerite rubble.

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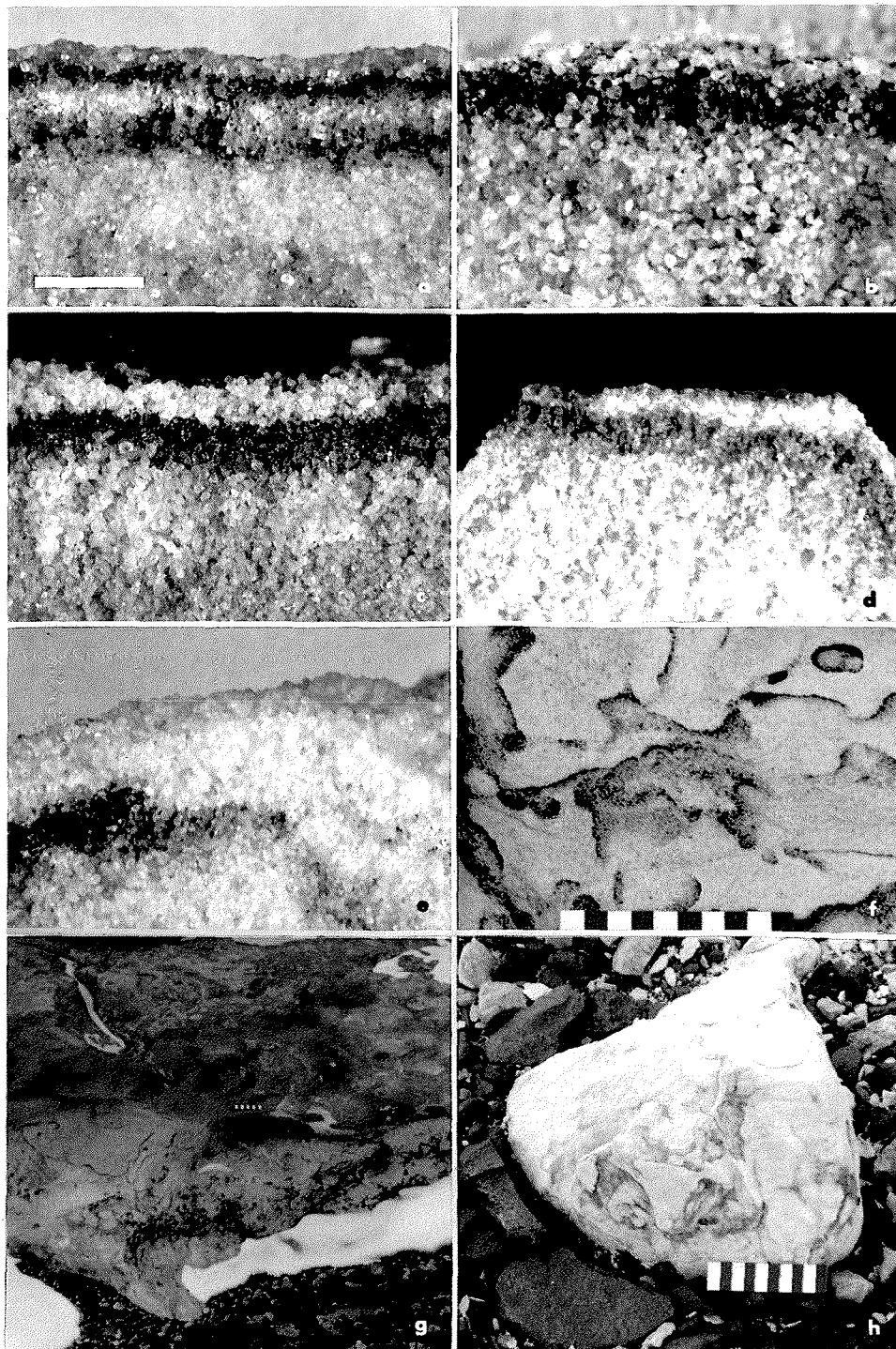
green alga *Hemichloris antarctica* Tschermak-Woess & Friedmann. Occasionally, hyaline fungal hyphae are present in this zone, apparently without forming a lichen.

Besides *Hemichloris,* other photosynthetic microorganisms may occasionally occur in the lower (green) zone. Often present, although in small quantities, is the cyanobacterium *Chroococcidiopsis* sp. (Fig. 2n, o). Much less frequent is the large cyanobacterium *Gloeocapsa* species 1 (Fig. 2c, d, i). There is definite, although not conspicuous, vertical zonation among these three photosynthetic organisms. When present, *Gloeocapsa* species 1 is within the lower levels of the *Hemichloris* zone. *Chroococcidiopsis* sp. is below *Gloeocpasa* but usually still within the confines of the *Hemichloris* zone. Occasionally, a separate *Chroococcidiopsis* zone is present below the *Hemichloris* zone: such a case is illustrated by FRIEDMANN (1977, Fig. 2). *Heterococcus endolithicus* Darling & Friedmann (DARLING et al. 1987) and *Stichococcus* sp. have been repeatedly isolated in enrichment cultures, but occur in very low numbers and are difficult to detect by microscopic examination of field material.

The green *Hemichloris* zone is usually present in the lichen-dominated community, but it is often inconspicuous and not visible to the unaided eye. In these cases, examination under the dissecting microscope usually reveals the prsence of *Hemichloris* (and *Chroococcidiopsis*) microcolonies on rock crystals.

The lichen-dominated community is the principal microbial community of the Ross Desert. It colonizes sandstones usually with a tan- to brown -to rust-colored primary iron stain (WEED 1985, WEED & NORTON in press). These iron stains are produced by the oxidation of the iron compounds coating the surface of the rock crystals.

The activity of the organisms results in a leaching of the iron compounds in the colonized zone, as well as in exfoliative weathering. This weathering results in a characteristic color mosaic pattern on the surface, a telltale sign of cryptoendolithic lichen colonization (Fig. 1g, FRIEDMANN 1982, WEED 1985, FRIEDMANN & WEED 1987, WEED & NORTON in press).

2.1.2 *Hemicheoris* community

The *Hemichloris* community is less commonly encountered. It appears as a single zone, formed by one photosynthetic organism, *Hemichloris antarctica.* It occurs typically on the lower face of overhanging rocks (TSCHERMAK-WOESS & FRIEDMANN 1984). The upper surfaces of these rocks are colonized by the lichen-dominated community, and the green *Hemichloris* zone of this community continues on the underside of the overhang, whereas the cryptoendolithic lichen zone terminates at the margin. The undersides of overhanging rocks do not receive direct solar radiation and are reached only by scattered or reflected light. Presumably, the ability of *Hemichloris* to survive at very low light intensities (NIENOW et al. 1988) enables this organism to occupy this habitat. The *Hemichloris* community does not produce an iron-free leached zone in the rock.

2.2 *Cyanobacterial Communities*

The common feature of these communities is that they consist of prokaryotic microorganisms, and, in this respect, they resemble hot-desert cryptoendolithic communities (FRIEDMANN & OCAMPO-FRIEDMANN 1984).

2.2.1 Red *Gloeocapsa* community

The red *Gloeocapsa* community (Fig. 1c) is macroscopically recognizable by a dark, purplish-red upper zone and characterized by the presence of red *Gloeocapsa* species 1 (Fig. 2c, d, i) and of *Gloeocapsa* species 7 (Fig 2i). Occasionally, *Gloeocapsa* 2 (Fig. 2e), *Gloeocapsa* species 3 (Fig. 2s), *Eucapsis* sp. (Fig. 2b), and *Microchaete* sp. (Fig. 2u) also occur in this zone. The lower zone, inconspicuous and not always present, is formed by *Gloeocapsa* species 8 (Fig. 2j).

The red *Gloeocapsa* community generally occurs in proximity to the lichen-dominated community. It is much less frequent than the latter and is typically present in two situations:

Fig. 2: Cyanobacteria in the Ross Desert cryptoendolithic communities; a: *Aphanocapsa* sp., scale = 10 μm (for all figures except i, n, o, t); b: *Eucapsis* sp.; c: *Gloeocapsa* species 1; d: *Gloeocapsa* species 1 (young cells); e: *Gloeocapsa* species 2; f: *Gloeocapsa* species 4; g: *Gloeocapsa* species 5; h: *Gloeocapsa* species 6; i: *Gloeocapsa* species 7 (yellow) among cells of *Gloeocapsa* species 1 (red), scale = 10 μm for (Figs. i and t); j: *Gloeocapsa* species 8; k—m: *Hormathonema* sp.; k: cell group (colony) from above; l, m: groups of cells with filament-like lamellated sheath (Nomarski interference); n, o: *Chroococcidiopsis* sp., scale = 10 μm (for figs. n, o); n: from rock sample A303, collected by W. V. Vishniac; o: from culture, CCMEE strain 168 (A303) isolated from material shown in n; p: *Lyngbya* sp.; q: *Anabaena* species 1; r: *Anabaena* species 2; s: *Gloeocapsa* species 3; t: *Anabaena* species 3; u: *Microchaete* sp. with cells of *Gloeocapsa* species 1 (red) and *Gloeocapsa* species 2 (grey).

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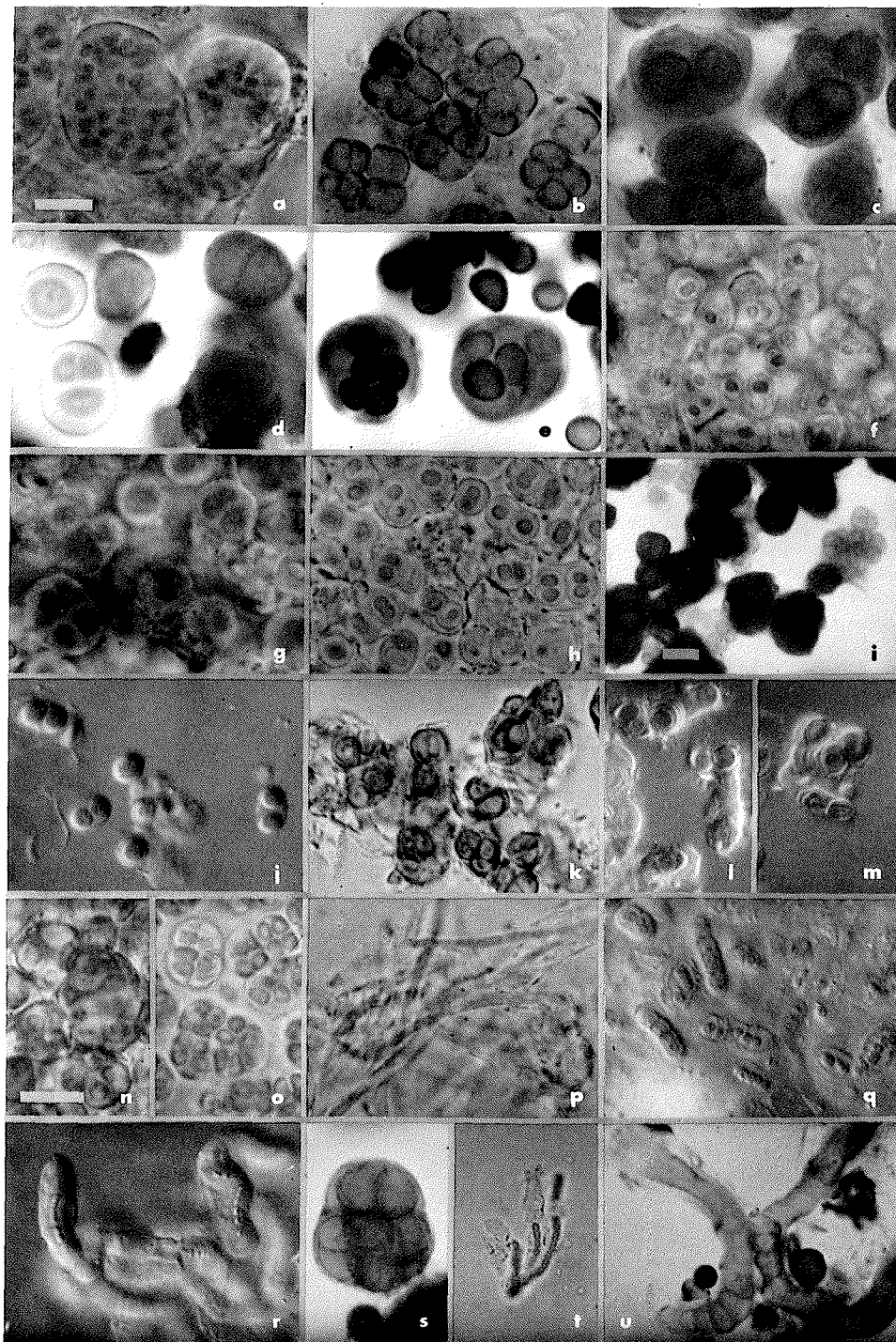
(1) On vertical faces of larger boulders where the horizontal face is usually occupied by the lichen-dominated community.

(2) Less frequently, near the margins of overhanging rock ledges occupied by the lichen-dominated community.

These overhanging rock ledges may thus be colonized by three different microbial communities: The upper surface by the lichen-dominated community, except at the margin where a zone a few centimeters to a few decimeters wide along the ledge is colonized by the red *Gloeocapsa* community, whereas the lower surface is colonized by the *Hemichloris* community. Intermediate stages between the lichen-dominated community and the red *Gloeocapsa* community also occur, consisting of a less well developed lichen upper zone and a dominant lower zone of red *Gloeocapsa*. The red *Gloeocapsa* community occurs, similar to the lichen-dominated community, in sandstones with a brownish primary iron stain, and it also produces an iron-leached zone in the substrate. This leached zone, however, is generally less conspicuous than the one produced by the lichen-dominated community.

2.2.2 *Hormathonema-Gloeocapsa* community
A characteristic feature of this community (Fig. 1b) is that it occurs in rocks that lack a primary iron stain. It produces exfoliative weathering that is somewhat reminiscent of a moiré pattern of blackish lines on the white rock surface (Fig. 1f-h). Macroscopically, both the upper and the lower colored zones are wider than those of the lichen-dominated community. They are also different in appearance from the lichen-dominated community in that the boundaries of the colored zones are not as sharply delimited. The color of the upper zone varies between brown and dark blackish grey. The characteristic organisms are *Hormathonema* sp. (Fig. 2k-m) and the dark grey *Gloeocapsa* species 2 (Fig. 2e): Either one or both of these organisms may be present. In addition, *Anabaena* species 1 (Fig. 2q), *Anabaena* species 2 (Fig. 2r), and less frequently *Gloeocapsa* species 3 (Fig. 2s) may occur in the upper zone.

The lower zone, usually separated from the upper one by a clear zone without cyanobacteria, is green and is characterized by *Aphanocapsa* sp. (Fig. 2a). This organism may be accompanied by *Gloeocpasa* species 4 (Fig. 2f), *Gloeocapsa* species 5 (Fig. 2g), the pink *Gloeocapsa* species 6 (Fig. 2h), *Anabaena* species 3 (Fig. 2t), and *Lyngbya* sp. (Fig. 2p).

To date, the *Hormathonema-Gloeocapsa* community has been found only on Battleship Promontory (Convoy Range). There, the white sandstone (without primary iron stain) that is colonized by this community forms a zone about 30—70 cm high along the bases of sandstone outcrops on dolerite rubble slopes (Fig. 1g) or occurs as sandstone clasts on these slopes (Fig. 1h). The slopes are frequently wetted by meltwater from the snow-covered Mt. Gran. The color of the sandstone in the outcrops (above the white zone) is that of the straw-to-tan iron stain, common in the Ross Desert. This white sandstone seems to occur only when in contact with the moist dolerite slope, and this pattern suggests that the lack of iron stain may be the result of a moisture gradient in the rock. Thus, the moisture gradient seems to be responsible for the distribution of the microbial communities. The transition between the lichen-dominated and the *Hormathonema-Gloeocapsa* community can be quite abrupt, as shown in Figure 1e.

2.2.3 *Chroococcidiopsis* community
The *Chroococcidiopsis* community (Fig. 1d) appears as a single, green or brownish zone in rocks with primary iron stain. It is formed by a single photosynthetic organism, *Chroococcidiopsis* sp. The first report on cryptoendolithic microorganisms in the Ross Desert (Tyrol Valley) was based on this community (FRIEDMANN & OCAMPO 1976). The *Chroococcidiopsis* community appears to be rare, and because of its scarcity, little is known about its ecology. The community seems to occur in comparatively extreme cold and dry habitats.

3. CYANOBACTERIA OF THE ROSS DESERT CRYPTOENDOLITHIC COMMUNITIES

The principal characteristics of 17 cyanobacterial types in these cryptoendolithic comunities are summarized in Tables 2a and 2b.

	Cells	Sheath and Colonies
Aphanocapsa sp.	Spherical or subspherical, 1.3–2.1 μm in diameter. Cyptolasm blue-green or pale blue-green, homogeneous.	Sheath hyaline, unlamellated, sometimes inflated. Colonies spherical to irregular, 7–52 X 20–74μm in diameter, with few to several hundred cells.
Eucapsis sp.	Spherical to ellipsoidal, in groups of 2 to 4 (8) cells, 2–3 X 1.5–3μm. Cyptoplasm brown, homogeneous.	Sheath brown, unlamellated. Colonies nearly cubic, 20–120 μm in size, composed of 8–32 (128), rarely more, regulary arranged groups of cells.
Gloeocapsa species 1	Spherical or subspherical, 3–12μm in diameter. Cyptoplasm reddish to purple, sometimes pale blue-green, homogeneous to granular with age.	Sheath reddish to deep red with conspicuous concentric lamellation with age. In later stages, the extended sheath may be shed. Colonies spherical or subspherical, 10–56 μm in diameter, with 2–4 (16), rarely more, cells, solitary or in aggregates.
Gloeocapsa species 2	Spherical or subspherical, 6–8 (13) μm in diameter. Cyptoplasm steel grey to purplish, especially in older cells, homogeneous to granular with age.	Sheath steel grey to purplish, becoming thicker, concentrically lamellated with age. Colonies spherical or subspherical, (12) 20–40 (60) μm in diameter, with 2–8 (32), rarely more, cells.
Gloeocapsa species 3	Spherical or subspherical, 5–8 μm in diameter. Cytoplasm yellowish to brown, homogeneous.	Sheath yellowish to brown, unlamellated. Colonies spherical or subspherical, 10–20 (32) μm in diameter, with 4–16 (32) cells.
Gloeocapsa species 4	Spherical or subspherical, 2–3 μm in diameter. Cytoplasm pale blue-green to blue-green, homogeneous.	Sheath hyaline, with conspicuous concentric lamellation. Colonies spherical or subspherical, 6–10 μm in diameter, with 2–4 (8) cells.
Gloeocapsa species 5	Spherical or subspherical, 3–5 μm in diameter. Cytoplasm blue-green, homogeneous.	Sheath hyaline, unlamellated. Colonies spherical or subspherical, 6–12 μm in diameter, with 2– 4 (8) cells.
Gloeocapsa species 6	Spherical or subspherical, 1.8–3.0 μm in diameter. Cytoplasm pink, homogeneous.	Sheath pale pink, lamellated. Colonies spherical or subspherical, 7–13 μm in diameter, with 2–4 (8) cells.
Gloeocapsa species 7	Spherical or subspherical, 1–2 μm in diameter. Cytoplasm yellow, homogeneous.	Sheat yellow, unlamellated. Colonies spherical or subspherical, 2–5 X 4–5 μm with 2–4 (8) cells.
Gloeocapsa species 8	Spherical or subspherical, 2–3 μm in diameter. Cytoplasm blue-green, homogeneous.	Sheath hyaline, unlamellated. Colonies spherical to ellipsoidal, 3–6 X 3–8 μm, with 2 (4) cells.
Hormathonema sp.	Spherical or subspherical, 1.2–2.4 (2–12 with sheath) μm in diameter. Cytoplasm pale blue-green, homogeneous.	Cells arranged in short filament-like groups, with often unilaterally thickened and lamellated sheath, but sometimes irregular and *Gloeocapsa*-like.

Tab. 2a: Principal characteristics of coccoid cyanobacteria of the cryptoendolithic communities in the Ross Desert. Note: *Gloeocapsa* species 7 always accompanies *Gloeocapsa* species 1.

Pleurocapsoid form		
	Baeocytes	Baeocyte mother cells
Chroococci-diopsis sp	Spherical or slightly irregular, 2–3 μm in diameter. Cytoplasm blue-green or yellowish, homogeneous.	Spherical or subspherical, up to 15 (20) μm in diameter, with 8–64, rarely more, baeocytes.

Filamentous forms		
	Cells and Trichomes	Filaments
Lyngbya sp.	Cells 1.3–2.3 μm in diameter, 2–8 μm long. Cytoplasm blue-green, homogeneous. Trichomes slightly constricted, not granulated at crosswalls.	3–5 μm in diameter and 15–95 (200) μm long. Sheath colorless, unlamellated, sometimes mucilaginous.
Anabaena species 1	Cells spherical or barrel-shaped, 1.0–1.2 μm in diameter. Cytoplasm blue-green or yellowish green, homogeneous.	3.5–5.5 μm in diameter, 5.4–16.6 μm long, staight or curved. Sheath yellow, thick, unlamellated. Heterocysts absent.
Anabaena species 2	Cells spherical or barrel-shaped, 0.8–1.2 μm in diameter. Cytoplasm pale blue-green, homogeneous.	3.9–8.8 μm in diameter. 5.6–55.5 μm long, straight or curved. Sheath unlamellated, inflated, colorless. Heterocysts absent.
Anabaena species 3	Cells spherical or barrel-shaped, 2–5 μm in diameter. Cytoplasm blue-green or dark blue-green, homogeneous.	5–15 μm in diameter and 20–50 (100) μm long, straight or curved. Sheath thick, unlamellated colorless. Heterocysts absent.
Microchaete sp.	Cells discoid, 7.0–11 μm in diameter and 2–4 μm long, end cells rounded. Cytoplasm yellow to brown, homogeneous. Trichomes constricted at crosswalls.	8–16 μm in diameter and 25–78 μm long. Sheath brown, firm, slightly lamellated, sometimes funnel-shaped at the apex. Heterocysts basal, sometimes intercalary, 7–8 μm in diameter.

Tab. 2b: Principal characteristics of pleurocapsoid and filamentous cyanobacteria of the cryptoendolithic communities in the Ross Desert. Note: *Anabaena* species 1 and *Anabaena* species 2 occur always together. The two forms are distinctly different in the structure of their sheaths.

4. ROCK HUMIDITY AND COMMUNITY DISTRIBUTION

The distribution of the principal communities appears to be controlled by the humidity level of the rock substrate. In dry typical desert habitats the rocks are colonized by the lichen-dominated community, whereas the *Hormat-honema-Gloeocapsa* community occurs in the frequently wetted white sandstone zone, encountered on Battleship Promontory. Water apparently affects rock chemistry, as is evident from the absence of primary stains in the frequently wetted rock colonized by the *Hormathonema-Gloeocapsa* community. The color of these rocks is off-white, yet the absence of primary stains is not an indication of absence of iron. A characteristic white sandstone

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sample from Battleship Promontory colonized by the *Hormathonema-Gloeocapsa* community contained 0.039% Fe_2O_3, compared with 0.132% Fe_2O_3 in a sample from Linnaeus Terrace colonized by the lichen-dominated community (proton-induced X-ray emission PIXE analysis was performed in the Department of Geology, Florida State University). Both of these values are within the range of iron contents reported by WEED (1985), and the absence of primary stain is probably an indication of the lower oxidation state of the iron compounds in the rock substrate.

In addition to rock color, there is also a difference between the pH values of the "dry" sandstones (with primary stain), colonized by the lichen-dominated or by the red *Gloeocapsa* community, and the "wet", white sandstones (without primary stain) inhabited by the *Hormathonema-Gloeocapsa* community. Table 3 summarizes the changes in pH in some rock outcrops or boulders, along with changes in rock-colonizing communities. The pH of rocks with primary stain ranged from 3.7 to 5.8, corresponding to the 4.5—5.5 range reported by WEED (1985). In contrast, white sandstones (with no primary stain) colonized by the *Hormathonema-Gloeocapsa* community had a pH range between 7.3 and 8.2. This difference suggests that pH may affect the oxidation state of the iron compounds, resulting in the color differences in the rocks.

	Sample	pH
Battleship Promontory, bedrock rising above dolerite rubble slope		
Lichen-dominated community, about 10 m above dolerite rubble	A867–27	3.8
	A867–26	4.0
Poorly developed lichen-dominated community,about 1 m above dolerite rubble	A856–58	5.8
Hormathonema-Gleocapsa community, about 20 cm above dolerite rubble	A856–55	8.15
Hormathonema-Gleocapsa community, about 5 cm above dolerite rubble	A856–54	8.2
Battleship Promontory, about 180 cm high boulder on dolerite rubble		
Lichen-dominated community, on top of boulder	A867–102	4.3
Red *Gloeocapsa* community on vertical wall of boulder, about 1.50 cm above dolerite rubble	A867–97	4.5
	A867–99	4.8
Hormathonema-Gleocapsa community, about 10 cm above dolerite rubble	A867–101	7.3
Battleship Promontory, rock ledge		
Lichen-dominated community, on upper surface	A867–29	4.45
	A867–29a	3.7
Red *Gloeocapsa* community, near edge of rock ledge, some lichens still present	A867–29b	4.15
	A867–30	4.3
	A867–29f	4.3
Hemichloris community, on lower surface of ledge	A867–28	3.9
Linnaeus Terrace		
Red *Gloeocapsa* community, near edge of rock ledge	A845–573	5.55

Tab. 3: Substrate pH values of crypthoendolithic microbial communities (measured in 1% KCl).

These differences in the physical properties of the substrate correlate well with the physiological requirements of the organisms. Lichens are well known to avoid the continued presence of liquid water and to be able to utilize atmospheric water vapor (BERTSCH 1966, LANGE 1969, PALMER 1987). In contrast, cyanobacteria and even desert forms require a saturated atmosphere or presence of liquid water (POTTS & FRIEDMANN 1981, LANGE et al. 1986, PALMER & FRIEDMANN in press). It is also common knowledge that, although cyanobacteria tolerate and, in fact, prefer an alkaline environment, green algae (such as the *Trebouxia* phycobiont of the cryptoendolithic lichens) prefer a pH that is neutral or lower. Thus, the combinations of liquid water with alkalinity (white sandstone) and absence of liquid water with acidity (sandstone with iron stain) create different microenvironments suitable for different communities.

5. ACKNOWLEDGEMENTS

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