

# 1 Biological Soil Crusts: Characteristics and Distribution

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## 1.1 Definition of Biological Soil Crusts

Biological soil crusts result from an intimate association between soil particles and cyanobacteria, algae, microfungi, lichens, and bryophytes (in different proportions) which live within, or immediately on top of, the uppermost millimeters of soil. Soil particles are aggregated through the presence and activity of these biota, and the resultant living crust covers the surface of the ground as a coherent layer (Fig. 1.1). This definition does not include communities where soil particles are not aggregated by these organisms (e.g., cyanobacterial/algal horizons in littoral sand and mudflats), where organisms are not in close contact with the soil surface (e.g., thick moss-lichen mats growing on top of decaying organic material, as in boreal regions), nor where the majority of the biomass is above the soil surface (e.g., large club-moss mats found in North American grasslands or dense stands of fruticose lichens, such as *Niebla* and *Teloschistes* species from the coastal fog deserts of California and of Namibia, respectively). However, the boundaries between the latter communities and biological soil crusts are fluid. In a similar fashion, there is no strict dividing line between the cyanobacterial, green algal, and fungal species that occur in soil-crust communities, yet are also found in a multitude of additional habitats (e.g., intertidal mats, tree trunks and leaves, rock faces).

Multiple names have been applied to biological soil crusts. These communities have been referred to as cryptogamic, cryptobiotic, microbiotic, microfloral, microphytic, or organogenic soil crusts (see Harper and Marble 1988; West 1990). Evans and Johansen (1999) discuss the implication of the different expressions. In this Volume, we use the term biological soil crusts because it is the broadest term which clearly states that these crusts are dependent on the activity of living organisms, in contrast to physical or chemical crusts (see Chap. 15). In addition, the term biological soil crust lacks taxonomic implications, and thus is broadly applicable to all soil crusts, regardless of their species composition.

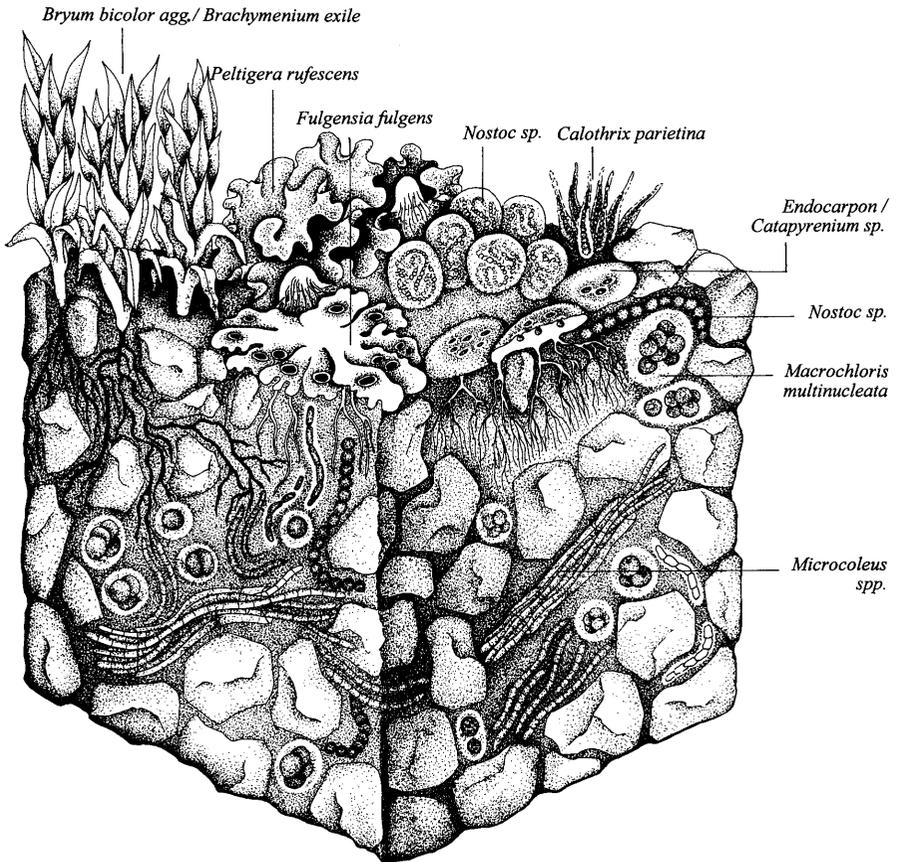
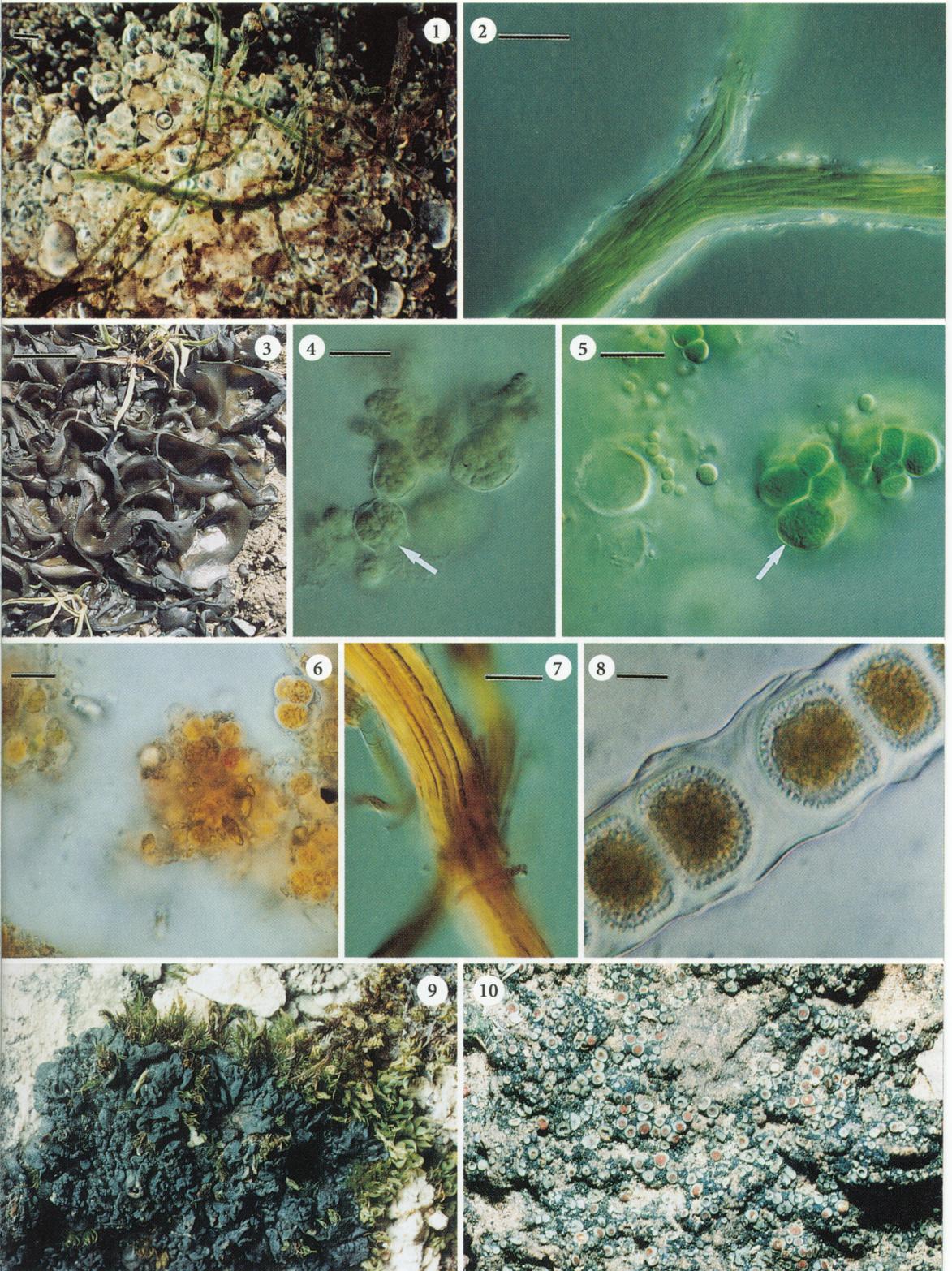
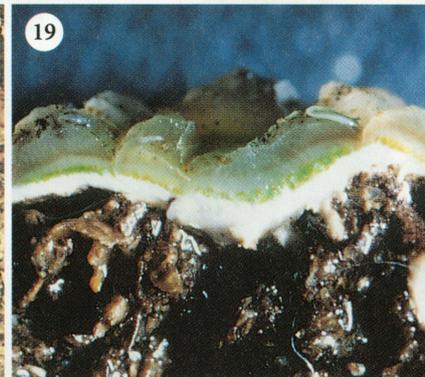
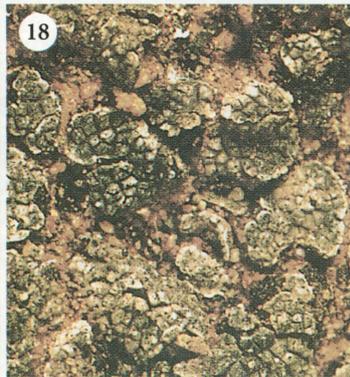
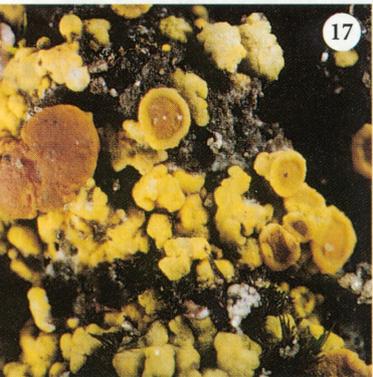
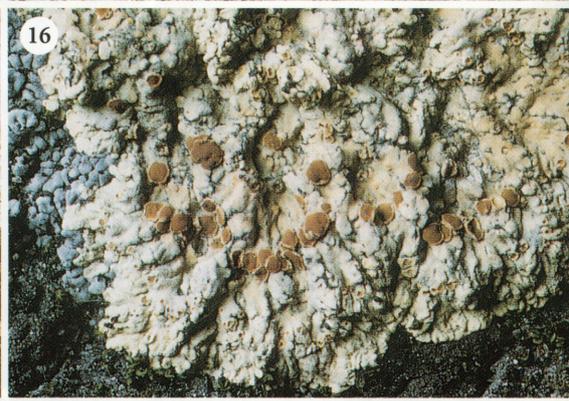
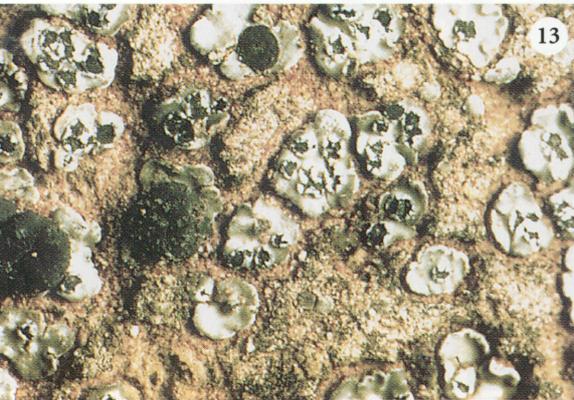


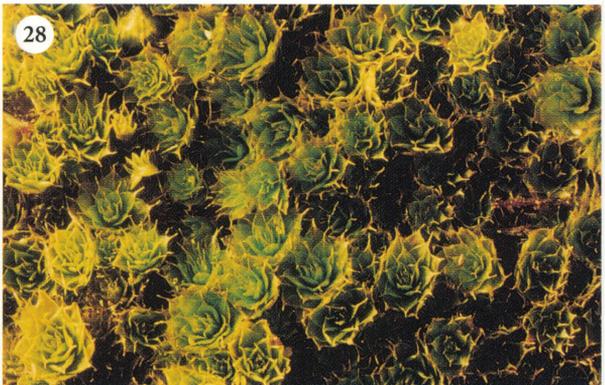
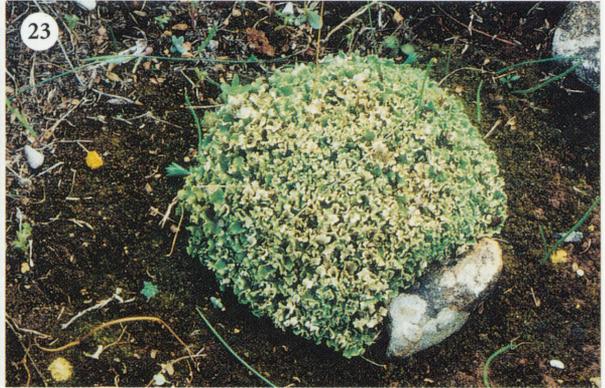
Fig. 1.1. Schematic block diagram of a biological soil crust with typical colonizers. Thickness of the layer about 3 mm, organisms not drawn to scale. (Illustration Renate Klein-Rödder)

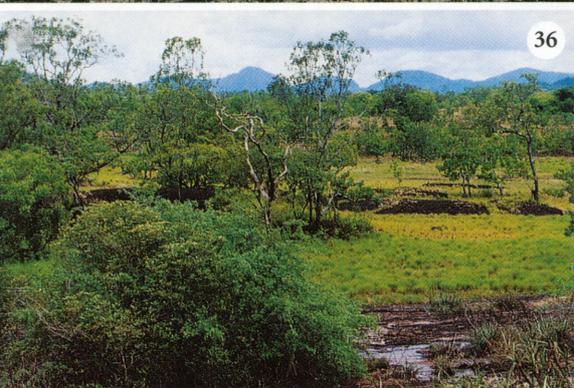
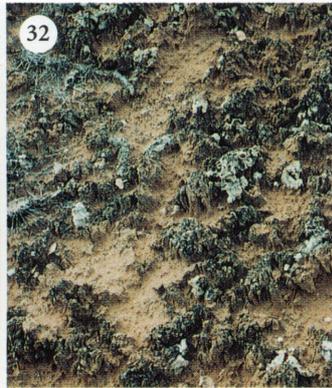
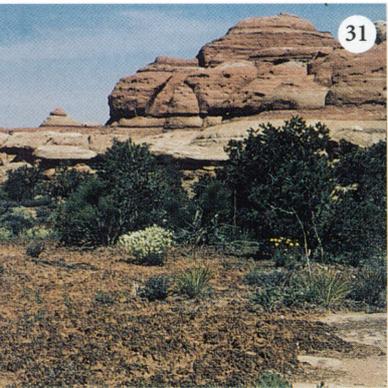
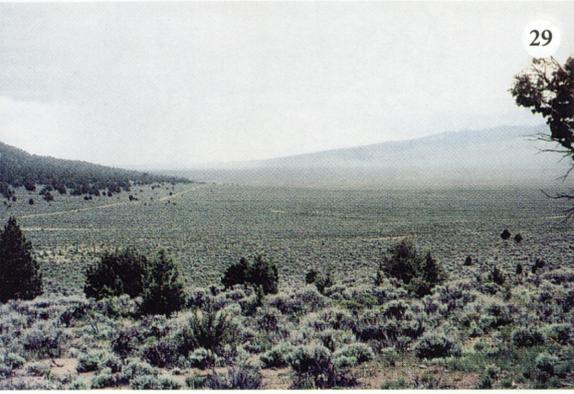
## 1.2 Taxonomic Components of Soil-Crust Communities (Photos 1–28)

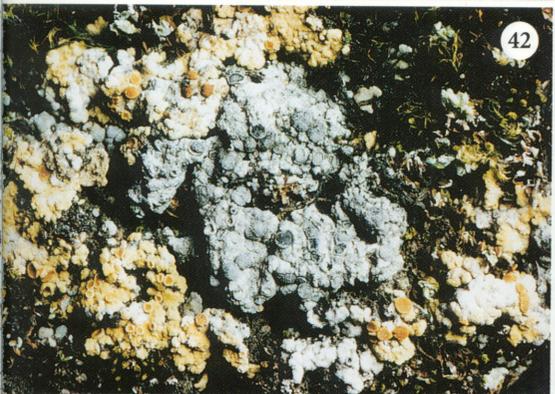
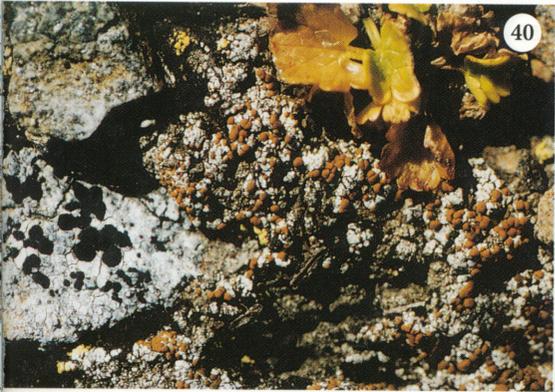
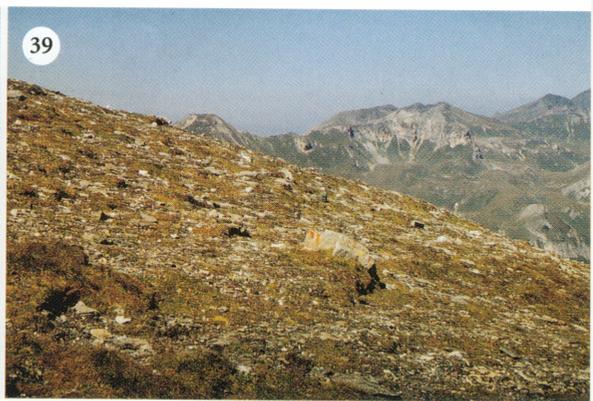
Cyanobacteria, and in particular species of the genus *Microcoleus* (Photos 1, 2), provide most of the cohesive quality of the biological soil crusts in arid and semiarid lands. As discussed in detail in Chapter 15, bundles of *Microcoleus* filaments are surrounded by extracellular sheaths which wind throughout the uppermost soil layers. When wet, the filaments glide out of their sheaths, and in a phototactic reaction, move up towards the soil surface. Upon drying, the filaments leave the surface, and the exposed filaments secrete new sheaths. The result of this frequent movement is copious sheath material dispersed

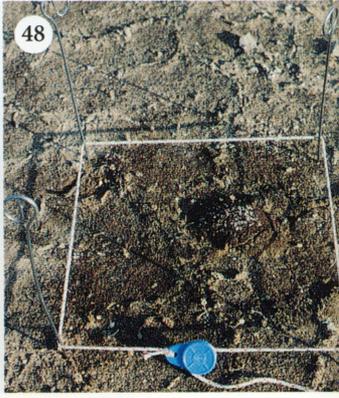
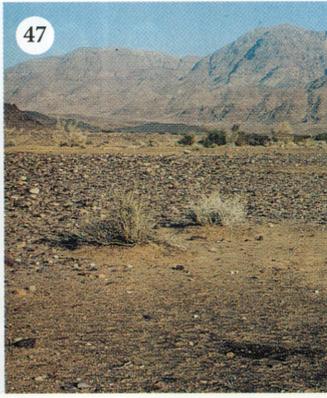


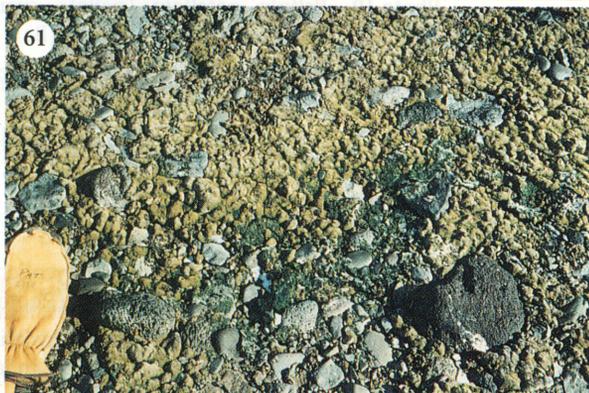
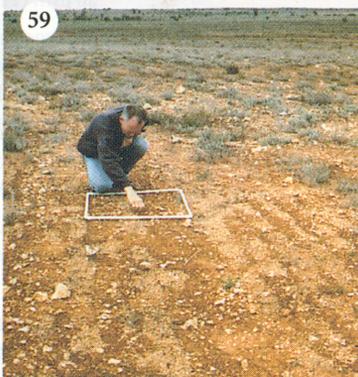












## Soil Crust Forming Organisms

- Photo 1.** Green filaments of *Microcoleus vaginatus* (Cyanobacteria) between quartz grains. Soil crust from Utah. Bar 0.1 mm. (Photo J.Belnap)
- Photo 2.** *Microcoleus paludosus* (Cyanobacteria) with numerous trichomes united in a common sheath. Soil crust from Tunisia. Bar 25  $\mu\text{m}$ . (Photo B.Büdel)
- Photo 3.** *Nostoc commune* (Cyanobacteria). Young, wet thalli on soil, Germany. Bar 20 mm. (Photo O.L.Lange)
- Photo 4.** *Chroococidiopsis* sp. (Cyanobacteria) showing baeocytes (arrow). Hypolithic habitat, Namib Desert, Namibia. Bar 20  $\mu\text{m}$ . (Photo B.Büdel)
- Photo 5.** *Pleurocapsa minor* (Cyanobacteria) pseudofilaments with baeocyte formation in one cell (arrow). Hypolithic habitat, Namib Desert, Namibia. Bar 20  $\mu\text{m}$ . (Photo B.Büdel)
- Photo 6.** *Macrochloris multinucleata* (Chlorophyta). Photo shows dry cells a few minutes after wetting. Soil crust from the Negev Desert, Israel. Bar 20  $\mu\text{m}$ . (Photo B.Büdel)
- Photo 7.** *Schizothrix telephoroides* (Cyanobacteria) trichomes in a typically reddish colored, common sheath. Soil crust from the humid savanna along the Orinoco, Venezuela. Bar 20  $\mu\text{m}$ . (Photo B.Büdel)
- Photo 8.** *Zygonium ericetorum* (Chlorophyta) cells with characteristic plastids and cell wall. Soil crust from a forest margin, Germany. Bar 10  $\mu\text{m}$ . (Photo B.Büdel)
- Photo 9.** *Collema tenax* (gelatinous cyanolichen) hydrated thallus on mosses. Soil crust in local steppe formation, Germany. (Photo H.Ullrich)
- Photo 10.** *Peltula patellata* (peltate cyanolichen) with whitish thallus and red apothecia. Sonoran Desert (Baja California, Mexico). (Photo B.Büdel)
- Photo 11.** *Lecidella crystallina* (crustose-areolated phycolichen). Namib Desert, Namibia. (Photo H.Zellner)
- Photo 12.** *Squamarina lentigera* (squamulose phycolichen) and *Tortella* cf. *inclinata* (Musci). Local steppe formation, Germany. (Photo H.Ullrich)
- Photo 13.** *Buellia subcoronata* (placoid phycolichen). Semiarid Australia. (Photo D.J.Eldridge)
- Photo 14.** *Psora crenata* (placoid phycolichen) with laminal pycnidia. Sonoran Desert (Baja California, Mexico). (Photo B.Büdel)
- Photo 15.** *Baeomyces placophyllus* (phycolichen with crustose-squamulose thallus and upright podetia). Clearing in a *Fagus sylvatica* forest, Germany. (Photo B.Büdel)
- Photo 16.** Phycolichens *Fulgensia fulgens* (yellow-whitish, crustose-squamulose) and *Toninia sedifolia* (bluish, bullate; left corner). Local steppe formation, Germany. (Photo H.Ullrich)
- Photo 17.** *Fulgensia bracteata* var. *alpina* (crustose-granular phycolichen). Alpine steppe formation, Austria. (Photo R.Türk)
- Photo 18.** *Eremastrella crystallifera* (placoid phycolichen; Fensterflechte or window lichen). Semiarid Australia. (Photo D.J.Eldridge)

- Photo 19.** *Eremastrella crystallifera* cross section, showing the transparent upper cortex above the algal layer, and with the underlying medulla. South Africa. Bar 0.5 mm. (Photo B.Büdel)
- Photo 20.** *Xanthomaculina convoluta*, a vagrant, foliose phycolichen in the dry, rolled (black) and in the wet, unrolled (green) state. Namib Desert, Namibia. (Photo O.L.Lange)
- Photo 21.** *Catapyrenium squamulosum* (placoid phycolichen) and *Riccia* sp. (Hepaticae; notice wet, unfolded leaflets). Dry savanna in North Transvaal, South Africa. (Photo B.Büdel)
- Photo 22.** *Cladonia convoluta* (foliose phycolichen). Mediterranean shrub, Cyprus, dry. (Photo O.L.Lange)
- Photo 23.** The same specimen as Photo 22, after moistening. (Photo O.L.Lange)
- Photo 24.** *Peltigera rufescens* (lobated cyanolichen). Local steppe formation, Germany. (Photo B.Büdel)
- Photo 25.** *Exorotheca holstii* (Hepaticae, Marchantiales) with air-chambers. Namib Desert, Namibia. (Photo B.Büdel)
- Photo 26.** *Campylopus introflexus* (Musci). Soil crusts on the margins of higher rainfall areas, east Australia. (Photo D.J.Eldridge)
- Photo 27.** *Gigaspermum repens* (Musci), small male and larger female individuals. Soil crusts throughout dry Australia. (Photo D.J.Eldridge)
- Photo 28.** *Bryum campylothecium* (Musci). Southern Australia, predominantly in woodlands and low shrublands. (Photo D.J.Eldridge)

## Landscapes and Habitats of Soil-Crust Occurrence

### The Americas

- Photo 29.** Eastern Oregon: *Artemisia tridentata* shrub-steppe with extensive soil crusts in interspaces. (Photo J.Belnap)
- Photo 30.** Same location as Photo 29: rolling soil crust with mosses and lichens. (Photo J.Belnap)
- Photo 31.** Colorado Plateau, Utah: pinnacled soil crusts in pinyon-juniper woodland. (Photo O.L.Lange)
- Photo 32.** Similar location as Photo 31: pinnacled soil crust with white *Diploschistes muscorum* and light green *Squamarina lentigera* (phycolichens). (Photo O.L.Lange)
- Photo 33.** Same location as Photo 31: pinnacled soil crust with *Psora cerebriformis* (white phycolichen). (Photo O.L.Lange)
- Photo 34.** Sonoran Desert flood plain (Baja California, Mexico): soil crusts in succulent bush. (Photo B.Büdel)
- Photo 35.** Same location as Photo 34: rugose soil crust with *Peltula richardsii* (dark green cyanolichen with maroon apothecia). (Photo B.Büdel)
- Photo 36.** Venezuela: humid savanna with *Trachypogon* grass. (Photo B.Büdel)
- Photo 37.** Same location as Photo 36: cyanobacterial *Schizothrix*-dominated soil crust. (Photo B.Büdel)

## Europe and Asia

- Photo 38.** Alps, Austria, Großglockner area: alpine mat vegetation with soil crusts in interspaces, 2700 m a.s.l. (Photo R.Türk)
- Photo 39.** Alps, Austria, Hochtor: alpine cold desert with soil crusts 2630 m a.s.l. (Photo R.Türk)
- Photo 40.** Same location as Photo 39: alpine soil crust with *Protoblastenia terricola*, whitish phycolichen with brown apothecia. (Photo R.Türk)
- Photo 41.** Local steppe formation with soil crusts in a typical German landscape, near Goslar. (Photo H.Ullrich)
- Photo 42.** Similar location as Photo 41: lichen soil crust with phycolichens *Buellia epigaea* (bluish white) and yellow *Fulgensia bracteata*, gypsic soil. (Photo H.Ullrich)
- Photo 43.** Germany, clearing in a *Fagus sylvatica* forest: successional soil crust dominated by the green alga *Zygonium ericetorum*. (Photo B.Büdel)
- Photo 44.** China, Ganzu Province: dwarf shrub-steppe (*Artemisia* and *Haloxylon*) with extensive rugose crusts formed by cyanobacteria and lichens. (Photo O.L.Lange)
- Photo 45.** Same location as Photo 44: soil crusts composed of the cyanobacteria *Nostoc flagelliforme* (arrow), phycolichens *Psora* sp. (red) and *Diploschistes* (white), and the black cyanolichen *Collema* sp. (Photo O.L.Lange)
- Photo 46.** A special Chinese meal prepared with black cyanobacterium *Nostoc flagelliforme* (Facai) in a baked, sliced eggroll. (Photo O.L.Lange)

## Middle East and Africa

- Photo 47.** Jordan, Wadi Arava: gravel desert with extensive moss crust. (Photo W.Frey)
- Photo 48.** Same location as Photo 47: moss soil crust formed by *Crossidio-laevipili-Toruletum-atrovirentis* association. (Photo W.Frey)
- Photo 49.** Israel (Negev Desert) Nizzana: smooth soil crust on dunes between *Cornulaca monacantha*. (Photo R.Bornkamm)
- Photo 50.** Similar location as Photo 50: smooth soil crust, dominated by the cyanobacterium *Microcoleus sociatus*, (Photo G.Kidron)
- Photo 51.** Africa, Namib Desert: extensive areas covered by rugose lichen-dominated soil crusts. (Photo O.L.Lange)
- Photo 52.** Similar location as Photo 51: rugose soil crusts with phycolichens *Lecidella crystallina* (whitish crust), *Xanthoparmelia walteri* (green, foliose) and *Xanthomaculina hottentotta* (blackish, foliose). (Photo O.L.Lange)
- Photo 53.** South Africa, Knersvlakte: shrub desert paved with quartz pebbles and lichen cyanobacteria-dominated soil crusts. (Photo B.Büdel)
- Photo 54.** Same location as Photo 53: soil crust with the red phycolichen *Psora decipiens* and quartz pebbles. (Photo B.Büdel)
- Photo 55.** Zimbabwe *Brachystegia* woodland with rugose soil crusts in interspaces. (Photo J.Belnap)
- Photo 56.** Same location as Photo 55: cyanobacterial (*Porphyrosiphon notarisii*)-dominated soil crust with some mosses. (Photo J.Belnap)

**Australia, Antarctica**

- Photo 57.** South Australia, eucalypt-mallee woodland with extensive cover and diversity of soil crust organisms. (Photo D.J.Eldridge)
- Photo 58.** Similar location as Photo 55: soil crust rich in phycolichens (e.g., *Diploschistes*, *Endocarpon* spp.) and mosses (e.g., *Didymodon torquatus*, *Desmatodon convolutus*). (Photo D.J.Eldridge)
- Photo 59.** South Australia, *Atriplex vesicaria* dominated shrubland: recovering soil crusts after topsoil removal more than 35 years ago. (Photo D.J.Eldridge)
- Photo 60.** Antarctica, Victoria Land, Hallett Station: flush of moss and algae in front of a penguin rookery. (Photo O.L.Lange)
- Photo 61.** Same location as Photo 60: soil crust composed of the moss *Bryum subrotundifolium* and the green alga *Prasiola* sp. (dark green). (Photo O.L.Lange)

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throughout the uppermost soil layers. As the sheath material is sticky, it adheres to, and aggregates, soil particles. The cohesive quality of these crusts can be easily seen when the surface of a desert soil is broken. Rather than breaking into individual soil particles, the soil breaks into larger pieces. If these pieces are held aloft, small soil clumps can be seen dangling down, held in place by cyanobacterial sheaths.

Taxonomy of the crust-forming *Microcoleus* species is still in the state of flux. *Microcoleus chthonoplastes* Thuret and *M. vaginatus* (Vauch.) Gom. are the two most frequent soil-crust species. While *M. chthonoplastes* prefers habitats with higher salinity (see Chap. 17), *M. vaginatus* is the main biomass contributor in many desert soil crusts. Recent studies using 16S rDNA sequencing (F. Garcia-Pichel, A. López-Cortéz, and U. Nübel, unpubl.) revealed that all samples of *M. vaginatus* coming from different localities of the world (Utah, California, Spain, and Israel) are virtually identical. They represent a 'good species', forming a monophyletic, deeply branched taxonomic cluster. However, this *M. vaginatus* cluster is more related to the filamentous cyanobacterium *Trichodesmium* than to the *M. chthonoplastes* cluster. The strains of the third soil-crust species, *M. sociatus* W. et G.S. West from Israel and Utah, are also identical. They form yet another distinct cluster that is not closely related to either *M. vaginatus* or *M. chthonoplastes*. Thus, the present genus *Microcoleus* seems to be polyphylous in nature and may be split into several genera in the future. However, further research is needed for such decisions, and in the present Volume the classic taxonomy will be maintained.

In addition to *Microcoleus*, cyanobacteria with single filaments also occur in biological soil crusts. *Nostoc* species are common in crusts, growing both within and on top of the soil. Sheets of *Nostoc commune* (Photo 3) and the horse hair-like, vagrant threads of *Nostoc flagelliforme* (Photo 45) spend a substantial period of their life cycle lying loose on soil surfaces in almost all

types of habitats (including the Arctic, tropics, and deserts). These species may be the only soil-crust organisms used for human food (Photo 46). *Scytonema* and *Calothrix* spp., with falsely branching trichomes, are frequent. Unicellular species are represented by the coenobia-forming (many cells in a common slime matrix) genus *Gloeocapsa*, and by single-celled Chroococcales (Photo 4). While all soil-crust cyanobacteria contribute carbon to soils, many also contribute nitrogen as well (Chap. 18–20).

Eukaryotic algae are represented mainly by coccoid species (e.g., of the genera *Chlorococcum*, *Macrochloris*, and *Stichococcus*, Photos 5, 6). In addition to these Chlorophyta, Euglenophyta and Chromophyta of the classes Tribophyceae and Diatomophyceae are also reported (see Johansen 1993). As a whole, hundreds of different species of cyanobacteria and eukaryotic algae are associated with biological soil crusts (Evans and Johansen 1999). Due to their limited biomass, the majority of these species, although widespread in distribution, are usually of secondary importance in the formation of crusts. The same is true for most of the bacteria which have been isolated from soil crusts. However, while little is known about fungal species found in crusts, they often contribute significantly to soil aggregate formation (Chap. 13).

Unlike the endodaphnic (subterranean) soil cyanobacteria and algae, the epedaphic lichens and bryophytes have almost all of their photosynthetic tissue on or above the soil surface (Fig. 1.1). Both phycolichens (with green algal photobionts) and cyanolichens (with cyanobacterial photobionts) with different growth forms (as defined by Jahns 1988) are found. Crustose lichens cover the soil with an appressed, more or less even, but discontinuous, layer of thalli. More or less isolated, crustose thallus scales occur in placoid genera like *Psora*, *Buellia* or *Trapelia* spp. (Photos 13, 14, 18, 21, 33, 54), and shield-like scales can form peltate thalli which are attached by a central holdfast, as in the genera *Endocarpon* or *Peltula* (Photos 10, 35). When thalli are more continuous, as in *Diploschistes* or *Lecidella*, the thallus surface is usually divided in small areoles (Photos 11, 40, 42, see frontispiece). Squamulose species such as *Squamarina* represent a transition to the foliose lichens; here, the margins of the individual thallus lobes are raised above the substrate (Photos 12, 15, 16). Foliose soil-crust lichens are exemplified by species of *Peltigera* (Photo 24). The transition to the fruticose form is represented by *Peltula* and *Toninia* spp. (Photos 10, 16), both with inflated thallus lobes, while examples of soil crust fruticose species include *Cladonia* (Photos 22, 23) or *Cladia* species. A special growth form associated with soil-crust communities in steppes and deserts are erratic and vagrant lichens (Wanderflechten) that have no attachment to the ground (Elenkin 1901; Rosentreter 1993), such as *Xanthoparmelia* spp. in North America and in the Asian steppes, *Chondropsis semiviridis* in Australia and New Zealand, *Xanthomaculina convoluta* in Namibia (Photo 20), and the different types of manna lichens (Crum 1993; see Chap. 9). Most of the lichens mentioned so far are heteromerous in structure,

i.e., their thallus is stratified in definite layers. There are also several important soil-crust cyanolichens with unstratified (homoiomorous) thalli and a gelatinous consistency. Examples include the genera *Collema* (Photo 9), *Gloeoheppia*, *Peccania*, and *Gonohymenia*.

Soil lichens have soil-anchoring structures (such as rhizoptae, rhizinae, and rhizomorphs, see Poelt and Baumgärtner 1964; Sanders 1994), which penetrate the uppermost soil layers. One type of these appendages is shown in Fig. 1.2 for *Buellia epigaea* (see Photo 42). Thin, corticated, and branched rhizomorphs (Rhizinenstränge) originating from the lower side of the thallus squamules extend for 4 to 5 mm into the soil. These strands are densely covered with a fine tomentum of rhizinae and single hyphae (Hyphenfilz) which fill the soil matrix. Thicker rhizomorphs of other species (e.g., *Toninia sedifolia*, Fig. 1.3; see Photo 16) connect the epedaphic thallus squamules with each other. They form a dense, subterranean network of fungal material, intimately connected to the soil particles. In *Psora cerebriformis* (see Photo 33) this system of rhizomorphs and rhizinae can penetrate soil down to 14 mm (O.L. Lange, unpubl.). While these structures are not known to transport water or nutrients, they firmly fasten the lichens to the soil, and thus enable them to withstand the erosive forces of wind and water. In addition, their subterranean structures contribute decisively to soil stability.

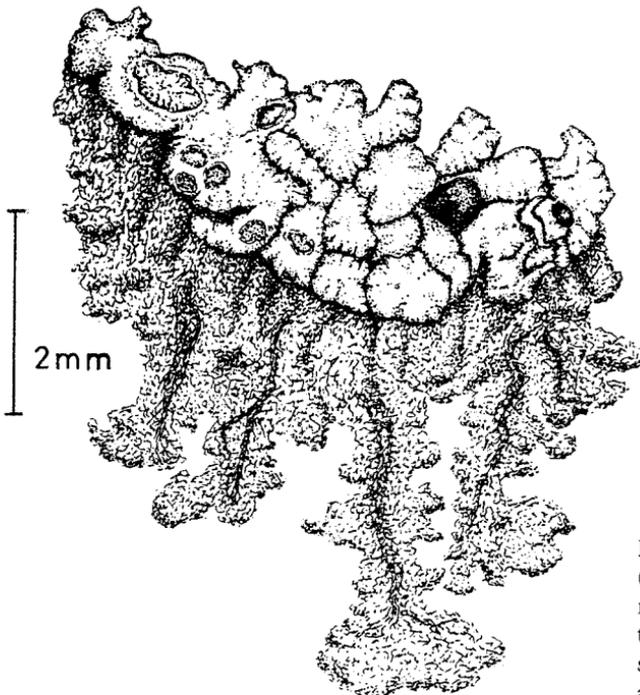
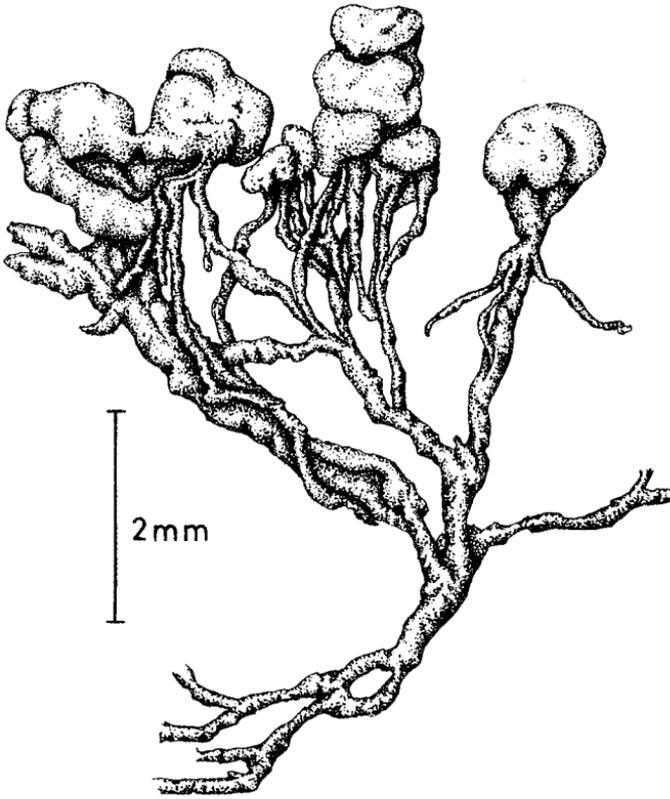


Fig. 1.2. *Buellia epigaea* (phycolichen) with thin rhizomorphs covered with tomentum of rhizinae and single hyphae. (After Poelt and Baumgärtner 1964)



**Fig. 1.3.** *Toninia sedifolia* (phycolichen) with system of branched rhizomorphs, which develop a tomentum of rhizinae at their ends, which is not shown. (After Poelt and Baumgärtner 1964)

The presence of bryophytes usually characterizes the more moist habitats of biological soil crusts. Both annual and perennial representatives of the Musci (true mosses; Photos 26, 27, 28, 48, 61) and the Hepaticae (thallose and leafy liverworts; Photos 21, 25) occur in soil-crust communities. Eldridge and Tozer (1996) report 56 bryophyte species (41 mosses, 15 liverworts) associated with biological soil crusts in semiarid and arid eastern Australia (see also Eldridge and Tozer 1997). However, the majority of publications dealing with arid-land bryophytes do not report their affiliation to soil-crust communities. Thus, a general overview about typical growth forms involved in soil-crust formation is not yet possible. The Pottiaceae seem to be the most abundant family associated with soil-crust habitats, and are represented by genera like *Aloina*, *Barbula*, *Crossidium*, *Pottia*, and *Tortula*. *Riccia* (Photo 21) seems to be the most important liverwort genus present in soil-crust communities. Frey and Kürschner (1988, 1991a) conducted extensive studies on ecology and life strategies of the terrestrial bryophyte vegetation of the Arabian Peninsula and in the Judean Desert (Israel), and described soil-crust habitats for many communities.

Terrestrial bryophytes are attached to the soil by rhizoids that often grow down more than 10 mm. Thallose liverworts such as *Riccia* (Photo 21) are closely appressed to the ground by a dense mat of unicellular rhizoids which form aggregates with the soil particles. In most of the mosses, the lower parts of the stems, together with their rhizoids, are involved in the anchoring process. Species such as *Gigaspermum mouretii* (Photo 27) have subterranean, rhizome-like, persistent main axes creeping through the soil, and under favorable conditions, above-ground lateral branches with stems and leaves (Frey and Kürschner 1991b). In addition, multibranched, subterranean moss protonemata are interspersed throughout the soil-crust matrix. These structures become intimately bound with the soil particles and contribute to the stability of the uppermost soil layers. In contrast to most soil-crust lichens, some mosses grow up through small amounts of newly deposited sand or dust (see Fig. 15.2b).

### 1.3 Habitats and Distribution of Soil-Crust Communities (Photos 29–61)

As soil-crust organisms have a limited ability to grow upwards from the soil surface, they are generally unable to compete with phanerogamous plants for light. Consequently, crust development is limited where climate conditions permit development of a closed vascular plant canopy or thick litter layers (Chap. 21). Thus, in arctic, boreal, temperate, and tropical regions, crusts occur only where the overstory cover is sparse or disappears due to limited water or local disturbance. Locally limited water facilitates crust development in dunes, in local steppe formations of Europe and Asia, in open woodlands (e.g., pine barrens of the southeast US), and within the discontinuous, evergreen mediterranean vegetation found worldwide. Following disturbance such as treefall or volcanic eruptions, crust organisms are generally the first to colonize.

Crust organisms have low moisture requirements, and their ability to utilize small rainfall events, snow melt, fog, and/or dew as water sources enables them to exist where moisture deficit limits vascular plant cover and productivity. In these low-productivity environments, the biological crusts colonize gaps left open by higher vegetation. This is true on a global, regional, landscape, and microsite scale (Chaps. 12, 16, 17); thus, crust communities occur in a large variety of phanerogamic formations in many different vegetation zones worldwide. Well-developed crusts occur in winter-cold steppes and grassland regions throughout the world. However, the most conspicuous development of crusts occurs in hot, cool, and cold semiarid and arid areas where plants are widely spaced. Vegetational communities in these

regions range from evergreen and deciduous woodlands, salt-bush communities, grassland, shrub, and succulent formations to areas with fixed dunes or regions where vascular plants are restricted to water-collecting depressions. Soil-crust communities also colonize the spaces between vascular plants in alpine areas and polar regions (see Part I). A selection of typical soil-crust habitats in different vegetation formations around the world are depicted in Photos 29–45 and 47–81.

Since all soil-crust biota are only metabolically active when wet, moister habitats (e.g., under plant canopies, under thin plant litter, or on northern exposures) in dry regions are favored by most crust species. Mosses and liverworts are often only found in such microhabitats, due to higher moisture requirements than lichens and cyanobacteria. These latter two groups are found both in the moister microhabitats as well as in more exposed, drier microhabitats. Soil-crust communities in areas with higher effective precipitation or those under vascular plants are often dominated by mosses, while in drier habitats they are dominated by lichens, cyanobacteria, and green algae (West 1990). Desert habitats with fog and dew (as the Namib, see Chap. 9, and the Central Negev Desert) favor phycolichens, whereas lack of dew, less rain, and higher temperatures (as in the Arava Valley, Dead Sea area) favor cyanolichens (Galun et al. 1982; see Chap. 18). Under still more extreme conditions, soil-crust communities consist almost exclusively of endodaphnic cyanobacteria.

Successional stages of crust communities can be distinguished (Chap. 27). Large filamentous cyanobacteria generally colonize first, followed by smaller cyanobacteria and green algae. After soil surfaces have stabilized, lichens and mosses appear. In temperate and tropical regions, these organisms influence soil formation as the vascular vegetation becomes re-established, a process which can last for decades. Under arid and semiarid conditions, where water limits vascular plant cover, crusts remain as the final stage of succession in plant interspaces (see Chaps. 21, 27).

Biological soil crusts are found on almost all soil types, as they can colonize soils with high to low levels of nutrients and soil salts, as well as a wide variety of soil textures. They are, however, limited on clay soils with a high shrink-swell coefficient. Soil pH and chemistry influence the composition of the crust communities. Green algae are favored on more acidic soils and/or in areas with higher effective precipitation. Areas with alkaline soils, high salt content, and/or lower effective precipitation favor cyanobacteria (see Chap. 17). Lichens grow across the pH gradient, although species composition may change (Chap. 2). Extensive moss and lichen cover is found on highly stable soils, such as gypsum and calcite, which also have high water-holding capacity and high levels of phosphorus and sulfur. Nitrogen-fixing species have been found to prefer sites with low soil N (Starks et al. 1981). The highly mobile and larger cyanobacteria (such as *Microcoleus* spp.) are generally dominant where

sediments are less stable, such as coarse sandy soils or in recently disturbed areas (Belnap 1993). Because the smaller cyanobacteria, green algae, lichens, and some mosses cannot grow up through large amounts of deposited sediment, they are generally found on either more inherently stable surfaces (e.g., alluvial or gypsiferous soils), or on soil surfaces initially stabilized by subterranean cyanobacteria (Chap. 27).

A frequent phenomenon in arid regions is the often almost luxurious, hypolithic growth of cyanobacteria and microalgae on the lower surface of translucent quartz pebbles on the desert surface (Fensteralgen or window algae; Vogel 1955). These organisms profit from dew condensation, which accumulates below the stones. Diatoms (Rumrich et al. 1989) and lichens (Schubert 1982) also colonize this microhabitat. These stones are tightly glued to the soil surface by these organisms, and thus contribute to soil surface stability.

## 1.4 Functional Adaptations of Soil-Crust Organisms

Given the wide range of vegetation types in which soil crusts occur, and given the different types of biological soil crusts (see Sect. 1.5), the similarity of the general appearance of soil-crust communities and the combination of growth forms involved worldwide is impressive. Many comparable structures and functions occur amongst nonrelated taxa both locally and globally, indicating that adaptation to the soil surface environment has produced a parallel response among these divergent taxa and implying convergent evolutionary trends. As an example, Vogel (1955) describes three placoid soil-crust lichens from South Africa with almost identical morphological features, very similar anatomical thallus structures, and similar functional adaptations, despite belonging to quite different taxonomic groups (species of the genera *Lecidea*, *Endocarpon*, and *Toninia*; Fig. 1.4).

Another striking feature is the taxonomic similarity of soil-crust communities worldwide (Chap. 12). There are many genera, and even some species, of cyanobacteria, algae, lichens, and bryophytes which occur on almost all continents. For example, the taxonomically well-defined lichen *Psora decipiens* (Hedwig) Hoffm. (Schneider 1979; Timdal 1986) is found on soil crusts in North America, Mexico, Africa, around the Mediterranean Sea, in Europe, throughout the Middle East, in India, in many areas of Asia, in Australia, New Zealand, and even in the high Arctic and the nival belt of the Alps. The species *Collema tenax*, *C. coccophorum*, and *Catapyrenium squamulosum* have a similarly widespread distribution (see Part I). Thus, on a worldwide basis, the soil-crust communities not only resemble each other with respect to convergent features, but also contain a significant portion of common taxa on both the

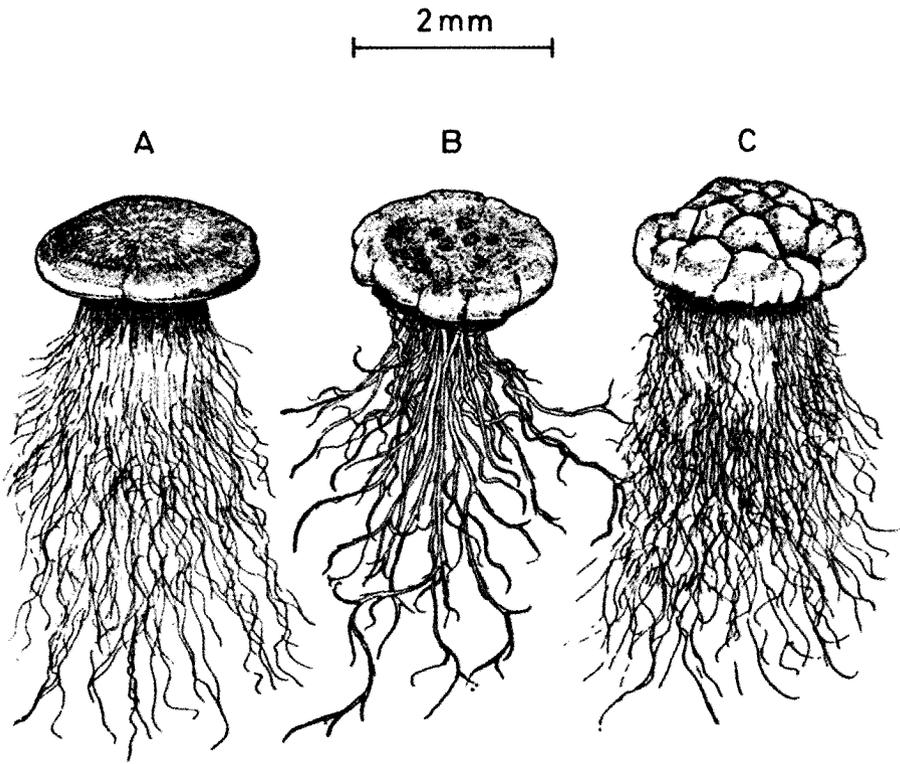


Fig. 1.4A-C. Convergent growth forms of soil lichens in South Africa: thalli of *Lecidea* (A), *Endocarpon* (B), and *Toninia* (C) sp. with rhizinae and hyphae. (After Vogel 1955)

generic and species level. This high degree of taxonomic similarity occurs in spite of crusts occurring in climatic zones ranging from hot deserts to polar regions, indicating that many crust taxa possess a broad ecological amplitude, while being highly specialized for the habitat at the soil surface.

The microenvironment in which the soil-crust biota are found (the uppermost millimeters of soil in relatively unshaded sites) is one of the most extreme habitats for autotrophic organisms on earth. The soil surface is a place of radiant energy conversion, and is where the highest and lowest temperatures occur within the soil-atmosphere profile. Temperatures up to almost 70 °C have been measured in terrestrial lichen thalli in a local steppe formation under temperate climatic conditions (southwest Germany; Lange 1953), and freezing temperatures can fall below -20 °C at the same site. Thus, for soil-crust organisms, the ability to tolerate extreme temperatures is one of the necessary requirements for existence. Indeed, when dehydrated, their distribution is not limited by even the most extreme environmental tempera-

tures. In a study by Lange (1953), terrestrial species from European temperate steppe formations belonged to the most resistant of all lichens tested. Viability of lichen photobionts was not impaired after 30 min of experimental exposure to 90°C (*Squamarina cartilaginea*, *S. lentigera*) or even 100°C (*Peltigera rufescens*, *Cladonia pocillum*). Desiccated soil-crust mosses showed similar heat-resistance limits (Lange 1955): from 100°C (*Tortella nitida*, *Ceratodon purpureus*) to 110°C (*Barbula gracilis*). Volk (1979) reported that soil-crust liverworts (*Riccia* spp. and *Exormothesca* sp.) from Namibia survived a treatment of several hours at 100°C. In contrast to desiccated organisms, the heat resistance of hydrated lichens and mosses is much lower, highlighting the importance of evaporative cooling in avoiding heat damage when direct sun radiation warms up a hydrated thallus.

In accordance with their habitat requirements, the photosynthetic metabolism of soil-crust lichens is adjusted to relatively high temperatures. This is especially true for the homoiomerous cyanolichen *Collema tenax* from Utah (Lange et al. 1998). In addition, net photosynthesis of phycolichens can also occur at extremely low temperatures. A *Diploschistes* species and *Cladonia convoluta* from a Mediterranean soil-crust community maintained low, but measurable, net photosynthesis down to a thallus temperature of -11.5 and -22°C respectively (Lange 1965; see Chap. 18). This is in agreement with the seemingly unlimited cold resistance of many lichens (Kappen and Lange 1972).

Poikilohydric soil-crust colonizers are often exposed to long periods of desiccation between infrequent moistening events. Dry weight-related water content of lichen thalli can reach 5% or less, terminating all metabolic processes. Many cyanobacteria, algae, lichens, and mosses tolerate strong experimental desiccation for extended periods (Bewley and Krochko 1982). *Cladonia convoluta* from a soil-crust site in southwest Germany was not impaired after 56 weeks of experimental drying (Lange 1953). *Nostoc flagelliforme* and *N. commune* from terrestrial habitats in China recovered after a drought period of 2 years with respiration, photosynthesis, and nitrogen fixation reactivating in that order (Scherer et al. 1984). Volk (1984) reported that *Riccia canescens* survived 7 years of desiccation. The stress hormone ABA is involved in induction of desiccation tolerance with bryophytes (Hartung and Gimmler 1994). This was extensively studied for the extremely xerophilic soil-crust liverwort *Exormothesca holstii* (Marchantiales, see Photo 25) from the Namib Desert by Hellwege et al. (1994).

Any anabolic metabolism of poikilohydric soil-crust organisms needs sufficient hydration. The periods of time under moistened, active conditions are short; often, lack of water is the limiting factor for existence. Many physiological and morphological features of poikilohydric organisms are viewed as adaptive strategies to prolong active periods and/or to make growth and production more efficient (see general reviews by Kappen 1973, 1988 and

Rogers 1977 for lichens; Proctor 1981 for bryophytes). Examples of such adaptations include the high water-holding capacity of some lichen thalli ("succulence" of gelatinous lichens, Galun 1963), and the special water-conducting and storing structures, glass hairs, and revolute leaf margins (to reduce transpirational water loss) of desert mosses (Frey and Kürschner 1991b, 1998). Phycolichens are capable of utilizing extremely small amounts of water for photosynthetic activity, and are able to use water vapor for reactivation (Chap. 18). This is not the case with soil-crust mosses (Rundel and Lange 1980), thus accounting for their absence or rarity in hyperarid environments.

Epedaphic crust organisms are also exposed to high levels of irradiance, further stressing these organisms. In fact, photoinhibition was observed in the Antarctic when soil-crust mosses were exposed to cycles of freezing and thawing (Lovelock et al. 1995; T.G.A. Green, pers. comm.). Soil-crust organisms have developed a variety of strategies to protect themselves against damaging effects of excessive radiation. Desiccation presents one effective photoprotective mechanism. Desiccated thalli of shade-adapted *Peltigera rufescens* from a local steppe formation near Würzburg survived experimental treatments of high light without any impairment, in contrast to hydrated specimens (Demmig-Adams et al. 1990a). Some low moisture content and/or long extended periods of exposure to high light can decrease the susceptibility of lichens to excessive light (Solhaug and Gauslaa 1996; Gauslaa and Solhaug 1999).

The photobionts of soil-crust lichens are covered by an upper fungal cortex and epinecral layer which, through their structure and pigmentation, reflect and absorb radiation. This may help the sensitive autotrophs to avoid excessive radiation (Rikkinen 1995). Indeed, only a fraction of incident light is transmitted through the cortex of many lichen thalli. For the soil-crust species *Psora crenata* and *P. decipiens* from the Sonoran Desert, only about 50 % of photosynthetically active radiation reaches the upper part of the photobiont layer (Dietz et al. 2000). Much lower degrees of transmittance are reported from *Peltula* species from South Africa and Mexico, where 89 to 93 % of incident radiation is absorbed by the fungal cortex, including the upper part of the photobiont layer (Büdel and Lange 1994). Thickness, structure, and pigmentation of the upper cortex of soil-crust lichens clearly show adaptive features to the light environment of their habitat (Vogel 1955; Kappen 1973; Dietz et al. 2000). Hygrochastic thallus movements, often found in lobate soil-crust lichens such as *Chondropsis viridis*, *Xanthomaculina convoluta*, or *Cladonia convoluta*, are interpreted as photoprotective (see Rogers 1977; Büdel and Wessels 1986). The flat thallus lobes curl when dry, so that the surface area exposed to insolation is reduced and the now upside-down photobiont layer is protected. Similar curling features are known for desert bryophytes and liverworts (Frey and Kürschner 1991b).

Free-living terrestrial cyanobacteria cells also protect themselves by synthesizing UV-screening pigments (Garcia-Pichel and Castenholz 1991, 1993; see Chap. 30). Seasonal time courses of pigment production are established in *Nostoc commune* colonies in terrestrial habitats (Bilger et al. 1997). The pigmentation in cyanolichens from high light-intensity habitats (including *Collema* cf. *coccophorum* from a soil crust in southern Utah) protects the photobiont from damaging UV rays (Büdel et al. 1997).

If excessive photosynthetic radiation is absorbed by hydrated lichens, green algal photobionts are able to effectively dissipate this energy. There is much evidence that the carotenoid zeaxanthin plays a decisive role in this process (Demmig-Adams et al. 1990b). Cyanobacteria lack the xanthophyll cycle needed to generate this carotenoid, and it is hypothesized that they instead use canthaxanthin for photoprotection (Leisner et al. 1994). Thallus content of canthaxanthin is positively correlated with light levels in the habitats of the studied lichens, and it is especially high in the soil-crust lichens *Gloeoheppia*, *Gonohymenia*, *Heppia*, and *Peccania* spp. of the Judean Desert (on the slopes of the Dead Sea, Leisner et al. 1993). The seasonal cycle of canthaxanthin production is also clearly correlated to the light received by *Peltigera rufescens* in a temperate terrestrial habitat (Lange et al. 1999).

## 1.5 Classification of Biological Soil Crusts

Biological soil crusts can be classified into several broad types based on habitat conditions, taxonomic composition, physical appearance, and function. The species composition of soil crusts is still not adequate for a large-scale floristic, phytosociological grouping of soil-crust communities. There have been several suggestions for crust classification using the growth forms of dominant species, soil substrate, and development processes as criteria (see West 1990). Soil algal growth types were defined by Komáromy (1976). Following Johansen (1993), Evans and Johansen (1999) typify crust formations encountered in the western United States. For the rangelands of Australia, Eldridge and Greene (1994) identify three forms of biological crusts: hypermorphs (above ground), perimorphs (at ground) and cryptomorphs (hidden below ground). Based on these earlier definitions, we propose a topographic classification of crust types that facilitates a worldwide comparison of crust morphology (Chap. 15). Four crust categories are used: smooth, rugose, pinnacled, and rolling. Smooth crusts are found in hot deserts where soils do not freeze, and are almost exclusively endedaphic cyanobacteria, algae and fungi (Photos 49, 50, 55, 56). Chemical crusting is also common in this crust type. The other three crust categories generally have epedaphic colonizers (lichens and mosses) in addition to endedaphic

autotrophs and fungi. Rugose crusts have low surface roughness (<2 cm), generally from scattered lichen and/or moss clumps (Photos 47, 48, 51, 52, 57, 58, 59). Under moister conditions in temperate regions, rugose crusts can also be dominated by an epedaphic layer of filamentous algae (such as *Zygonium*), which can penetrate 4 mm deep into the soil (Photos 8, 43). Pinnacled and rolling crusts occur only where soils freeze in winter. Pinnacled crusts are dominated by cyanobacteria, but locally can have up to 40% moss-lichen cover. Pinnacles range up to 15 cm high (Photos 31, 32, 33). Rolling crusts occur in regions where high precipitation results in heavy lichen-moss cover, and frost-heaving of these surfaces results in a gently rolling surface about 5 cm high (Photos 29, 30, 40, 41, 42, 44, 45). This classification, discussed in detail in Chapter 15, is a highly generalized scheme, and the four categories are connected by intermediate crust types.

## 1.6 Problems with Species Identification and Sampling

Sampling and describing soil-crust communities presents some fundamental difficulties. First, species identification for many crust components is problematic. For instance, few cyanobacterial, green algal, bacterial, or fungal genera have received the attention necessary to establish clear taxonomic relationships or to provide definitive identification criteria for the many forms a species can assume. Isolated cells or filaments are often found that cannot be determined with the commonly used identification techniques. In addition, many species may be present in insufficient numbers for identification. In these cases, culturing is necessary. However, even if firm taxonomic identification is possible, culturing cannot provide frequency or biomass estimates. Thus, characterization of the microbial components of soil crusts is difficult.

Second, lichens and bryophytes have received greater taxonomic attention than the microbial components. Nevertheless, many species can only be determined through microscopic examination, or by specialists. This often hinders fieldwork aiming at statistically sound descriptions of species composition of crust communities. Some attempts have been made to facilitate recognition of diversity of soil-crust biota by nonspecialists. Often, dominant genera or easily recognizable indicator species can be identified, allowing a general characterization of crust communities. Morphological groups of soil-crust organisms can also be defined, which is being successfully used for rangeland monitoring (Chap. 32).

Third, species composition and abundance can also vary drastically with season. Although perennial lichen and moss components generally show little change from season to season, ephemeral mosses and especially cyanobac-

terial and algal populations can show large seasonal fluctuations (Johansen and Rushforth 1986; see Chap. 28). Therefore, representative assessments of the ecological role of soil-crust components and spatial comparisons often require measurements be made in all seasons, and this is often difficult.

Lastly, it is rare that the scientist involved in characterizing the species composition of a soil crust is a specialist in all of the taxonomic groups occurring in a given community. This often results in varying levels of emphasis for different crust groups, depending on the investigator, and complicates comparisons between described crust communities. In addition, descriptions of the different components or functions of a given crust community are often published in journals of widely-separated disciplines (lichenology, phycology, bryology, ecology, geology, etc.), making collation of this information difficult.

## 1.7 Heterogeneous State of Knowledge in Different Geographic Areas

The intensity of study on the structure, function, and management of biological soil crusts has varied widely between different geographic areas. For example, there is a large literature on crusts in the western United States, Australia, and Israel, and yet very little on crusts in South America or Asia. It might be concluded that research has been concentrated in certain areas because crusts are more important or more apparent in those ecosystems. This is definitely not the case. The amount known about crusts in a given area reflects more the location of interested scientists, rather than the importance of the crust to a given ecosystem. Many remote regions have never even been surveyed for the presence of soil crusts. In addition, there are serious limitations for obtaining and evaluating local literature from large areas of the world, especially when results are published in languages like Russian or Chinese.

In the following chapters of Part I of this Volume, the different geographic areas are treated separately by appropriate specialists. The chapters summarize the actual state of available information. The disparity of information regarding biological soil-crust communities on different continents is immediately apparent. Further research on the role of soil crusts in understudied habitats is needed, especially in areas where human activities are accelerating.

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